The late Miocene macroflora of the La Cerdanya Basin (Eastern Pyrenees, Spain): towards a synthesis

by

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Abstract

The fossil plant-bearing beds of the Tortonian (late Miocene) intramontane basin of La Cerdanya (Eastern Pyrenees, Catalonia, Spain) have been investigated for more than a century, and 165 species from 12 outcrops have been described in previous publications. The sediments with rich plant fossil assemblages, which correspond to lacustrine diatomitic deposits, contain large numbers of plant remains, mainly leaf compressions and impressions. These assemblages are well preserved, a consequence of the rapid accumulation of plant remains in the sediments of the basin's ancient lake, and the often close proximity of its shores to wetland and upland vegetation. This paper provides a comprehensive taxonomic and nomenclatural review of the historic and new collections of late Miocene macroflora for the La Cerdanya Basin. Examination of the newer materials allowed emendments to be made to the diagnoses of *Abies saportana*, *Acer pyrenaicum*, *Alnus occidentalis*, *Quercus hispanica* and *Tilia vidali* provided by Rérolle for the basin at the end of the 19th century. In addition, 24 species of vascular plants are identified for the basin for the first time, including one horsetail, three conifers, 19 arboreal or bushy dicotyledonous angiosperms, and one monocotyledonous angiosperm. Indeed, this is the first time that *Cedrela heliconia* (Unger) Knobloch, *Decodon* sp., *Hedera* cf. *multinervis* Kolakovskii, *Mahonia* cf. *pseudosimplex* Kvaček & Walther, *Smilax* cf. *aspera* L. var. *fossilis* and *Ulmus* cf. *plurinervia* Unger have been recorded anywhere in the Iberian Peninsula. The La Cerdanya Basin plant assemblages of the late Miocene mainly consisted of conifers and deciduous broadleaved taxa of Arctotertiary origin; evergreen Palaeotropical elements were less well represented. This flora is similar to those recorded at coeval sites in northern Greece, northern Italy and central and eastern France. Within the Iberian Peninsula, the late Miocene macroflora reported for the nearby Seu d'Urgell Basin is the most similar.

1 Introduction

Our knowledge of the evolution and main characteristics of the flora and vegetation of the Neogene in the Iberian Peninsula is still fragmentary. Over recent decades, however, palaeobotanical studies have begun to clarify certain traits and features of the fossil floras of different periods (Barrón et al. 2010). One of these partially understood periods is the late Miocene – the prelude to the Pliocene, a time of marked floristic and climatic change in the Iberian Peninsula (Postigo-Mijarra et al. 2009). In this region, the palaeobotanical evidence indicates the vegetation of the late Miocene, which was eminently dry, to have been mainly one of open and steppe habitats, except in coastal areas and places with lakes or mountains (Barrón et al. 2010).

Although some important general characteristics of the Spanish late Miocene vegetation are known, an exhaustive revision of fossil floras is still necessary in order to reconstruct the Iberian ecosystems of this period. The La Cerdanya Basin is a very interesting late Miocene site in this respect, and numerous studies have been performed in the area over the last two centuries. The first palaeobotanical studies were undertaken in the 19th century by Rérolle (1884a, 1884b, 1885), who described 12 species and three varieties of vascular plants (mainly from leaf remains) for the first time. This work had a great impact on studies of other late Miocene and Pliocene western European floras performed at the end of the 19th and in the early 20th centuries (see e.g., Boulay 1890, Laurent & Marty 1908, Teixeira 1952, Grangeon 1958). Revisions of the La Cerdanya Basin's late Miocene macroflora (Villalta & Crusafont 1945, Menéndez Amor 1948, Menéndez Amor 1955, Álvarez Ramis & Golpe-Posse 1981, Sanz de Siria 1980a, Sanz de Siria 1985) notably increased the number of plant taxa recorded, which eventually reached 165 species. Later, however, after a thorough revision of the flora carried out as part of a doctoral thesis, Barrón (1996a) could only identify and describe 64 species. Other, more recent studies have only examined aspects of certain genera or families (Barrón 1992a, Barrón 1992b, Barrón 1996b, Barrón 1996c, Barrón 1998, Barrón & Diéguez 1994), leaves with preserved cuticles (Barrón & Diéguez 2005, Hably & Fernández-Marrón 2007), herbaceous remains (Postigo-Mijarra et al. 2003) and aquatic plants (Martín-Closas et al. 2006).

The late Miocene leaf flora of the basin may be one of the most characteristic of the time for southwestern Europe. However, though the varying interpretations of different author many doubts remain regarding the basin's true floristic composition. A review and re-evaluation of the work of Rérolle and other researchers of the 20th century is therefore needed.

The aims of the present paper are: (1) to provide new morphological and anatomical data, complementing the descriptions of certain taxa made by Rérolle, (2) to undertake a complete macrofloristic study of the late Miocene assemblages of the La Cerdanya Basin, while presenting a number of new taxa, and (3) to compare the studied macroflora with palaeobotanical data for neighbouring areas and central Europe. A complete revision of the palaeoclimatic aspects of the basin which include all the palynological data published for the basin would also be of great interest. This is not under the scope of this paper but it will be carried out in a future work.

2 Location of the study area and geological background

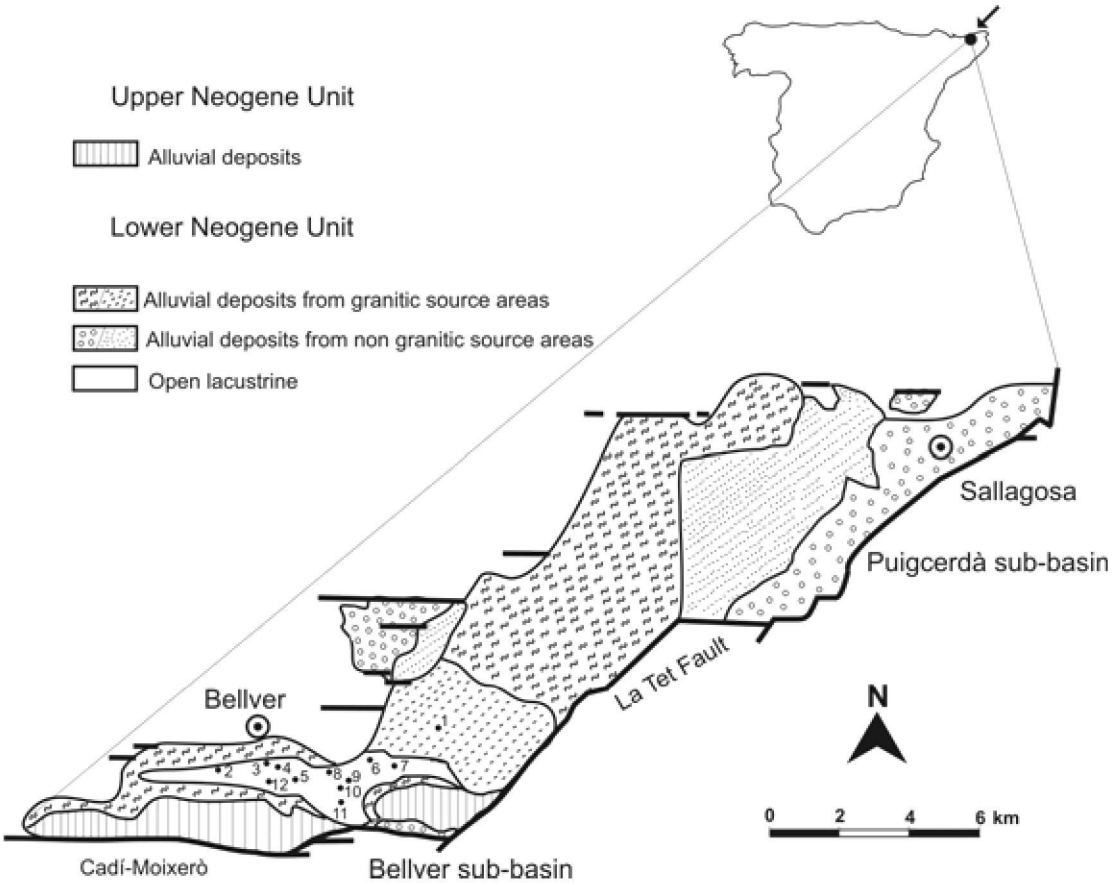
The La Cerdanya Basin is an ENE-WSW orientated half-graben in the Axial Zone of the eastern Pyrenees (in Catalonia, north-eastern Spain), located in the northwestern block of the La Tet fault (at its southern termination) (Roca 1986, Cabrera et al. 1988, Anadón et al. 1989). The Neogene infill of this basin consists of 400 to 1000 m of predominantly siliciclastic, muddy, sandy and conglomerate alluvial fan to fluvial sequences (Pous et al. 1986, Cabrera et al. 1988, Roca 1995).

Two depositional units have traditionally been distinguished within the siliciclastic materials. These correspond to two stages in the evolution of the Neogene basin, in which tectonics and sedimentation played important roles (Astre 1927, Roca & Santanach 1986, Cabrera et al. 1988, Roca 2002). The Lower Neogene Unit, which comprises the oldest (Tortonian [=Vallesian]; late Miocene) sediments (Déperet & Rérolle 1885, Golpe-Posse 1981, Agustí & Roca 1987) is responsible for the majority of the present outcrops in the basin, while the Upper Neogene Unit, of which the base is Messinian (= Turolian) in age (Agustí & Roca 1987, Agustí et al. 2006), is represented only at the basin's southern end.

This paper focuses on the macrofloral assemblages of the Lower Neogene Unit (400–800 m), where diatomites and thin lignite seams link respectively to open and marginal lacustrine palaeoenvironments (Roca 1995). Over the years, fossil plants have been collected from 12 surface outcrops close to the village of Bellver de Cerdanya (42°22'21"N, 1°46'38"E) (province of Lleida, Catalonia, Spain) (Text-fig. 1). The geographical location of these outcrops has been indicated in previous papers (Villalta & Crusafont 1945, Barrón 1996a, Martín-Closas et al. 2005, Barrón & Comas-Rengifo 2007). From a taphonomic viewpoint, most of the studied plant macroremains were collected from the so-called taphofacies of the lake and represent remains transported by water and wind (Martín-Closas 1995).

3 Material and methods

This work examines around two thousand fossilised plant remains, including 750 new specimens – a horsetail stem (1), leaves (710), bracts (1), fruits of dicotyledons (2), the leaf of a monocotyledon (1), a conifer shoot (1), seeds (16), seed scales (1) and female cones (17) – and those of the J.F. Villalta collection (Natural History Museum of Barcelona [NAT]) and of the J. Menéndez Amor collection (National Museum of Natural History [MNCN], Spanish National Research Council – CSIC, Madrid) that is the oldest for the basin still in existence. The original materials described by Rérolle (1884a, 1884b, 1885) no longer exist (Martín-Closas et al. 2006); neotypes of the taxonomically accepted fossil species were therefore designated from the F. Villalta and J. Menéndez Amor collections. Comparative recent material was consulted at the Royal Botanical Garden of Madrid (CSIC) and the School of Forestry Engineering, Universidad Politécnica de Madrid. The nomenclatural and taxonomic details of the text follow the International code of nomenclature for algae, fungi and plants (McNeill et al. 2012).



Text-fig. 1. Geological context of La Cerdanya Basin modified from Roca (1995) and Barrón & Comas-Rengifo (2007). The location of the studied outcrops is shown. 1. The opencast Sanavastre lignite mine, 2. Santa Eugenia outcrop, 3. Carrer de Bellver de Cerdanya outcrop, 4. Barranc de Salanca outcrop, 5. Torrent de Vilella outcrop, 6. Coll de Saig outcrop, 7. Prats outcrop, 8. Riu de Santa María outcrop, 9. Balltarga outcrop, 10. Beders outcrop, 11. Pedra outcrop, 12. Carrer de Pi outcrop.

Table 1. Taxa identified for the La Cerdanya Basin from macroremains. 1. Barrón (1996a); 2. Rérolle (1884a); 3. Menéndez Amor (1955); 4. Hably & Fernández Marrón (2007); 5. Barrón & Diéguez (2005); 6. Barrón (1996c); 7. Villalta & Crusafont (1945); 8. Rérolle (1884b); 9. Barrón & Diéguez (1994); 10. Solé Sabarís & Llopis Lladó (1947); 11. Martín-Closas et al. (2006); 12. Sanz de Siria (1980); 13. Diéguez et al. (1996); 14. Arroyo García (1995); 15. Barrón (1998); 16. Rérolle (1885); 17. Barrón (1992a); 18. Barrón (1996b); 19. Postigo-Mijarra et al. (2003); 20. Barrón (1992b); * This work. L: leaf, S: stem, F: fruit, I: inflorescence, IN: involucre. A: Arctotertiary; P: Palaeotropical; H: Pluriregional. Names in brackets are regarded as synonymous.

Taxa	Organ	Origin
Equisetum sp.*	S	H
Pteridium oeningense (Unger) Hantke[1] (*Pteris radobojana* Unger[2,3], *Pteris protogaea* Principi[3])	L	A
Osmunda parschlugiana Andreánszky[1] (*Osmunda strozzii* Gaudin[2,3])	L	A
Ginkgo adiantoides (Unger) Heer[4]	L	A
Abies saportana Rérolle emend.*	F	A
Cryptomeria anglica Boulter[5] (*Juniperus drupaceae* [Labill] var. *pliocenica* [2], *Taxodium distichum miocenicum* Heer[3], *Doliostrobus rerollei* Marion[3])	S/L	A
Cupressaceae gen. et sp. indet.[1,5] (*Glyptostrobus europaeus* Brogniart)[3]	S/L	A
Cupressaceae gen. et sp. indet.*	S/L	A
Pinaceae gen. et sp. indet.*	F	A
Pinus palaeostrobus Ettingshausen[3]	S/L	A
Pinus sp. (*Pinites* sp.[3,7], aff. *Pinus* sp.[1])	F	A
Torreya bilinica Saporta & Marion[5]	L	A
cf. *Tsuga* sp.*	C	A
Acer integerrimum (Viviani) Massalongo[1,18] (*Acer decipiens* A. Braun[3,7,8,10,14], *Acer laetum* C.A. Meyer *pliocenicum*[3,12,16], *Lygodium gaudinii* Heer[3], *Acer cappadocicum* Gledich[20])	L	A
Acer pyrenaicum Rérolle emend. *	L	A
Acer subcampestre Goeppert[1,18] (*Acer campestre* L.[3,14,20], *Acer* cf. *campestre* L.[7])	L	A
Acer sp. 1[1,18]	F	A
Acer sp. 2[1,18]	F	A
Alnus occidentalis Rérolle emend.*	L	A
Alnus sp.*	L	A
Aralia multifida Saporta[3] (aff. *Aralia* sp.[1])	F	P
Betula pseudoluminifera Givulescu (*Betula insignis* Gaudin[6], *Betula speciosa* Rérolle[2])	L	A
Buxus pliocenica Saporta & Marion[5] (*Buxus sempervirens* L. var. *ceretana* Rérolle[3,8], *Bumelia* sp.[8])	L	P
Caesalpinites sp.*	L	P
Carpinus betulus L. *fossilis* (*Carpinus grandis* Unger[1,6])	IN	A
Carpinus grandis Unger emend. Heer[6] (*Carpinus grandis* Unger p.p.[2], *Ostrya oeningensis* Heer[3], *Carpinus pyramidalis* (Goeppert) Heer[3], Betulaceae gen et sp.[6], *Ostrya oeningensis* Heer[7])	L	A
Carpinus neilreichii Kováts[6] (*Carpinus grandis* Unger p.p.[2])	F	A
Cedrela heliconia (Unger) Knobloch*	L	P
Ceratophyllum schrotzburgense Hantke[11] (cf. *Ranunculus* sp.[1])	S/L	H
Commelinidae incertae sedis[19] (*Rhizocaulon* sp.[3])	I	H
Commelinidae incertae sedis[19] (*Typha latissima* A. Braun in Heer[1,3,7,12])	L	H
Corylus sp.[6]	IN	A
Daphnogene polymorpha (A. Braun) Ettingshausen, (*Cinnamomum polymorphum* Heer[2,3,7,10], *Dicotiledonea* sp.[3], *Daphnogene* sp.[1])	L	P
Decodon sp.*	L	?

Dicotylophyllum sp.*	L	?
Dombeyopsis lobata Unger (*Tilia expansa* Saporta[8])	L	P
Fabaceae gen. et sp. indet.*	L	?
Fagus gussonii Massalongo[1,9,13] (*Fagus pliocenica* Saporta var. *ceretana* Rérolle[2,3,7,10,12], *Colutea macrophylla* Heer[3], *Castanea ungeri* Heer[3])	L	A
Fagus haidingeri Kovats sensu Knobloch (*Fagus* [*Castanea*?] cf. *castaneaefolia* Unger[3,7,10,14], *Fagus pristina* Saporta[1,3,9,12,13,14])	L	A
Fagus sp.[9] (*Punica granatum* L. var. *planchoni* Saporta[3])	F	A
Fraxinus numana Massalongo[1] (*Fraxinus* sp. p.p.[8], *Potamogeton rufescens* Schrad[3], *Fraxinus excelsior* Linné[17])	F	A
Hedera cf. *multinervis* Kolakovskii*	L	P
Laurophyllites sp.[5]	L	P
Laurophyllum pseudoprinceps Weyland & Kilpper[5] (*Daphnogene eugeniae* Barrón[1], *Quercus drymeja* Unger[1])	L	P
Laurophyllum sp. *	L	P
cf. *Laurophyllum* sp. *	L	?
Leguminocarpon sp. 1*	F	?
Leguminocarpon sp. 2*	F	?
Mahonia cf. *pseudosimplex* Kvaček & Walther*	L	P
cf. *Myrica* sp.*	L	P
Ostrya sp.[6]	IN	A
"*Parrotia*" *pristina* (Ettingshausen) Stur[3,16] (*Parrotia gracilis* Heer[3,16])	L	A
Poaceae gen et sp. indet.[1,19]	I	H
Populus tremulaefolia Saporta[1] (*Populus canescens* Sm. [pliocenica] Rérolle[3,8], *Populus tremula* L. [*pliocenica*][3,7,8])	L	A
Potamogeton orbiculare Rérolle[1,2,3,11]	L	H
Pterocarya paradisiaca (Unger) Iljinsk. (*Pterocarya denticulata* [C. O. Weber] Heer[3,7], Juglandaceae[1])	L	A
Quercus drymeja Unger[1,3,13,14] (*Quercus praeilex* Saporta[2], *Quercus drimeia* Unger[7,10], *Salix tenera* A. Braun[3,7,10], *Andromeda protogea* Unger[3], *Dryandroides* aff. *banksiaefolia* Heer[3], *Ficus lanceolata* Heer[3], *Mahonia malheurensis* Arnold[3], *Quercus praeilex* Saporta[3], *Sapindus dubius* Unger[3])	L	P
Quercus mediterranea Unger[1,7,15] (*Quercus crassipes* Heer[3], *Ilex cyclophylla* Unger[3])	L	P
Quercus hispanica Rérolle emend. *	L	A
Quercus neriifolia A. Braun ex Unger[3,7,10,14]	L	P
Quercus sp.*	L	¿
cf. *Quercus* sp.[15] (*Castanea palaeopumilla* Andrae[3,7,8,10], cf. *Castanea* sp.[1])	L	A
Rhamnaceae gen. et sp. indet.*	L	?
Rosaceae gen. et sp. indet.*	L	A
Salix lavateri A. Braun[1] (*Salix longa* A. Braun[12], *Salix angusta* A. Braun[12])	L	A
Smilax cf. *aspera* L. var. *fossilis**	L	P
Tilia vidali Rérolle emend. *	L	A
Trapa ceretana Rérolle emend. Wójcicki & Martín-Closas[11]	F	H
Ulmus cf. *plurinervia* Unger*	L	A
Ulmus sp.[1] (Ulmus braunii Heer[3])	F	A
Zelkova zelkovifolia (Unger) Bůžek & Kotlaba[1,13] (*Zelkova crenata* Spach[7,8,10], *Zelkova subkeaki* Rérolle[7,8], *Zelkova* [*Planera*] *ungeri* Ettingshausen[7], *Zelkova planera*[10], *Rhus pyrrhae* Unger[3], *Zanthoxylon serratum* Heer[3], *Zelkova ungeri* Ettingshausen[3,14])	L	A

All the examined plant fossils were collected from the laminated diatomites that crop out near the village of Bellver de Cerdanya. A significant part of the new material studied was recovered by one of the present authors of this study (E.B.) during doctoral thesis fieldwork. Currently, these specimens form part of the E. Barrón collection housed at the MNCN, Madrid (palaeobotanical collection: MNCNV). The remaining specimens belong to the collections of the following institutions: the Institut d'Estudis Ilerdencs - IEI, Lleida (general collection: BC); the Geological Museum of the Seminary of Barcelona (general collection: MGSB); the Geomining Museum, Spanish Geological Survey – IGME, Madrid (general collection: MGM); the NAT (general collection: MGB, and J.F. Villalta collection: MGBV); and the Institut Català de Paleontologia Miquel Crusafont – ICP, Sabadell (M. Llenás collection: CMLL, and J. Querol collection: CJQ). Both recent and historic collections were comprehensively examined.

These well-preserved fossils consisted of both compressions and impressions without cuticles. Their good state of preservation may be a consequence of the micritic nature of the sediments in which the fossils were found. Morphological features, especially shape of lamina, margin and venation, were used to describe the dicotyledonous leaves examined (Hickey 1973, Ash et al. 1999). The anatomical terminology used to describe the conifers follows that of Vidakovic (1991). Systematic assignment of angiosperms and author names of families follows the APG III (APG III 2009, Reveal & Chase 2011). Morphological studies were performed with a binocular microscope at magnifications of 4 to 40. Photographs of the specimens were taken using a NIKON D80 digital camera. Some epidermal features of the species *Tilia vidali* Rérolle emend. were studied using a FEI Inspect scanning electron microscope (SEM), working at low vacuum. This method was also applied to other specimens belonging to other species, but revealed no applicable results.

In the text, two adjectives are used to describe the palaeofloristic origin of the identified taxa: Arctotertiary and Palaeotropical. 'Arctotertiary' is applied to deciduous broadleaved woody plant elements, the ancestors of which developed in the circumarctic regions during the Late Cretaceous and early Palaeogene. 'Palaeotropical' is applied to nothophyllous evergreen broadleaved elements that were relatives of those that originated during the Late Cretaceous–Eocene in central Europe (Mai 1989, Mai 1991, Mai 1995).

Table 1 shows all the fully identified taxa for the La Cerdanya Basin and the resulting synonymies. Table 2 records significant taxa of uncertain presence in the basin.

Table 2. Taxa described for the La Cerdanya Basin by Villalta & Crusafont (1945) and Menéndez Amor (1955) from poorly preserved specimens; the presence of these taxa needs to be confirmed from better preserved material.

Taxon	References
Pirus phytali Unger	Menéndez Amor (1955)
Cotoneaster sp.	
Crataegus nicoletiana Heer	
Caesalpinia cf. *lepida* Heer	
Caesalpinia townsherdi Heer	
Caesalpinia micromera Heer	
Cassia ambigua Unger	
Cassia berenices Unger	
Cassia lignitum Unger	
Cassia palaeogea O.Weber	
Podogonium knorii (Al. Braun) Heer	
Podogonium hyellianum Heer	
Calpurnia europaea Saporta	
Leguminosites argutus Heer	
Leguminosites proserpinae Heer	
Leguminosites salicinus Heer	
Mimosites haeringianus Ettinghausen	
Terminalia miocenica Unger	
Hiraea expansa Heer	
Melastomites radobojanus Unger	
Salix cf. *denticulata* Heer	
Embothrium microspermum Heer	
Banksia deikeana Heer	
Banksia helvetica Heer	
Conospermum macrophyllum Ettingshausen	
Edwarsia parvifolia Heer	
Dyospyros cf. *anceps* Heer	Villalta & Crusafont (1945)

4 Systematic descriptions

Equisetaceae Richard ex De Candolle in Lamark & De Candolle 1805

Equisetum L. 1753a

Equisetum sp.

Pl. 1, Fig. 1

1996a *Equisetum* sp. – Barrón, pp. 51–52, text-fig. 4, pl. 1, fig. 4.

Material: MNCNV-4724, 4830. Specimens collected from the Coll de Saig and Carrer de Pi outcrops, respectively.

Description: Poorly preserved fragments ~1.5 cm long, consisting of a main stem, ~1.7 mm wide, divided into nodes and internodes. The internodal regions are ornamented with longitudinal ribs. The specimens show whorls of needle-like leaves. Specimen MNCNV-4830 shows rounded supranodal scars at the nodes.

Remarks: The poor state of preservation of the specimens prevents their comparison with extant and fossil *Equisetum* species. The first references to this genus for the La Cerdanya Basin were made in open nomenclature by Álvarez Ramis & Golpe-Posse (1981). In the Iberian Peninsula, *Equisetum* occurs occasionally in Oligocene and Miocene plant fossil assemblages (Sanz de Siria 1985, Sanz de Siria 1992, Barrón & Diéguez 2001, Barrón & Postigo-Mijarra 2011).

Cupressaceae Gray 1822

Cupressaceae gen. et sp. indet.

Pl. 1, Fig. 2

Material: MGB-47049. Specimen collected at an unknown site.

Description: Shoot, 21 mm long and 0.7–0.9 mm wide, with leaves departing at an angle of <65–75°; leaf arrangement opposite decussate with two marginal and two imbricated facial scale-like leaves; leaves pointed ovoid to rhomboidal with entire margin, 1.2–1.6 mm long and 1.2–1.5 mm wide; resin glands not visible; poorly preserved midveins in some marginal leaves.

Discussion: This specimen shows a clearly cupressoid leaf architecture very similar in shape, size and arrangement to several extant species of *Juniperus* L. (e.g., *J. chinensis* L. or *J. foetidissima* Willd.) and *Cupressus* L. (e.g., *C. sempervirens* L. or *C. goveniana* Gord. ex Lindl.) (Vidakovic 1991). It also shows certain morphological similarities to the North American species *Chamaecyparis lawsoniana* (Murr.) Parl., although the latter usually has lateral leaves with outspreading apices, a feature not observed in the studied specimen. However, this characteristic has been described in specimens with cuticles previously identified as Cupressaceae gen. et sp. indet. 1 (Barrón 1996a, Barrón & Diéguez 2005). Extant representatives of the genus *Thuja*, especially the species *T. orientalis* L., also show analogies with the studied specimen, such as small leaf size and the leaf arrangement. In the Iberian fossil record, the number of macroremains that belong without doubt to the family Cupressaceae is very small. On the basis of leaf shape, size and arrangement, the present specimen might be compared to MPV-259, assigned to *Juniperus* sp., from the Rubielos de Mora Basin that is early Miocene in age (Barrón & Diéguez 2001: pl. 2, fig. 6). The central European early Miocene species *Juniperus pauli* Kvaček shows branchlets with imbricated leaves that are also reminiscent of the studied specimen (Kvaček 2002: fig. 2G, fig. 3A–B). In addition, the leaf arrangement and the shape of the scale-like leaves render the specimen comparable to *Cupressus* sp. (identified with doubts) from the late early/early middle Miocene of Austria (Kovar-Eder et al. 2004: pl. 1, figs 17–19). Similar foliage has been associated with *Cupressus* seed cones from the early Miocene of Kymi and late Miocene of Vegora (Kvaček et al. 2002). Unfortunately, the lack of cones and cuticles does not allow the studied specimen to be attributed to any particular genus of Cupressaceae.

Pinaceae Spreng. ex F. Rudolphi 1830

Abies Mill. 1754

Abies saportana Rérolle emend.

Pl. 1, Figs 3–5

1884a *Abies saportana* Rérolle, pp. 182–184, pl. 3, fig. 4.

1955 *Abies saportana* Rérolle – Menéndez Amor (pars), pp. 44–45, pl. 16, fig. 5.

1996a aff. *Abies* sp. – Barrón, pp. 84–85, text-fig. 10, pl. 6, fig. 4.

Neotype: Specimen MGM-318M from the Villalta and Crusafont collection, selected herein, held at the Geomining Museum (IGME) (Pl. 1, Fig. 4).

Occurrence: Coll de Saig outcrop (42° 22′ 2″N, 1° 49′ 20″W), in the ditches of local road 1411, which runs through a diatomite bed.

Other material examined: MGBV-9780, 9793–9794, 47064; MGSB-40222, 40456, 48116; MNCNV-309, 3093, 4769–4770, 4775, 4777–4778, 4780. These specimens were collected from the Barranc de Salanca, Coll de Saig, Prats and Balltarga outcrops.

Original diagnosis: A. foliis linearibus rectis, longis, vix pedicellatis, obtusiusculis, nervo medio leniter prominulo; seminum ala magna, subquadrata, apice dilatata.

Emended diagnosis: Seeds, nearly obovate, held in a deep cup, fully covered by this cup only on one lateral side; seed-base not pointed; presence of a flap covering about ¼ of the seed on the front side; wings nearly triangular in shape.

Description: Seeds nearly obovate, 5–7 mm long, 2–5.5 mm wide, held in a deep cup, fully covered by this cup only on one lateral side; seed-base not pointed; resin vesicles not visible; presence of a flap covering about ¼ of the seed on the frontal side. Wings near triangular in shape, 6.3–7.8 mm long, 6.5–11 mm wide; apical margin straight or slightly convex; presence of fan-like diverging striation; ratio of the wing/seed length about 1.18.

Discussion: RÉROLLE (1884a: pl. 3, fig. 3) studied specimens of shoots with linear leaves and seeds in his identification of *Abies saportana*. The poor preservation of the present shoots and leaves in combination with the presence of other conifers with linear leaves such as *Tsuga*, *Cathaya* and *Picea* in the late Miocene La Cerdanya Basin (BARRÓN, 1996a), prevent these fossil remains from being clearly assigned to *Abies*. However, the features of the seeds correspond without doubt to those of this genus. The name *A. saportana* is therefore maintained. RÉROLLE drew two fossil seeds (1884a: pl. 3, fig. 4). The one on the left shows the features described above, whereas the one on the right may be a poorly preserved specimen given its rounded wing.

According to KVAČEK et al. (2002), the differentiation of seeds from conifers such as *Cedrus, Keteleeria* and *Abies* is not easy. However, the shape and size of the seed and its wing, the seed/wing length ratio (see FRANKIS 1988, VIDAKOVIC 1991) and the position of the seed in a deep cup on the wing of the studied specimens attribute them without doubt to the genus *Abies* and indeed to the species *A. saportana*. Similar fossils were described from French Neogene sediments as *Picea*? sp. (BOULAY 1892), *Abies ramesi* SAP. (SAPORTA 1879, MARTY 1903), *Abies* aff. *A. cephalonica* LOUD. and *Abies* sp. (GRANGEON 1958). *A. ramesi* was described from the late Miocene of Cantal (France) and was related to the extant east Asian fir *Abies cilicica* ANT. & K. CARR. However, the scant descriptions made by SAPORTA (1879) and MARTY (1903) prevent the relation of *A. ramesi* to the La Cerdanya Basin specimens. According to PALAMAREV (1989), *A. saportana* may be related to the extant species *Abies pinsapo* BOISS. and *A. cephalonica* LOUD; it is probably their ancestor. Taking into account the studies of VIDAKOVIC (1991) on recent firs, the longer, triangular-shaped seeds of *A. cephalonica* are quite different to those of the studied specimens. However, *A. pinsapo* also has near-obovate seeds about 6–10 mm long, and a wing twice the size of the seed. These features clearly coincide with those of the La Cerdanya Basin specimens. *A. alba* MILL. usually has longer seeds (7–13 mm) but with wings having twice the length of the seeds. Other extant firs such as *A. koreana* WILS., *A. fraseri* (PURSH) POIR., *A. veitchii* LINDL. and A. *grandis* LINDL. also have similar seeds (FRANKIS 1988, VIDAKOVIC 1991). The fossil species *Cedrus vivarensis* BOULAY, which was widespread in southern Europe during the late Miocene and Pliocene, also commonly have a broad wing and oval seed, but a seed/wing ratio typical of the genus *Cedrus* (KVAČEK et al. 2002).

Tsuga (ENDL.) CARR. 1855

cf. *Tsuga* sp.

Pl. 1, Figs 6–7

1955 *Abies saportana* RÉROLLE– MENÉNDEZ AMOR (pars), pp. 44–45, pl. 16, fig. 4.

1955 *Pinus palaeostrobus* (ETTINGSHAUSEN) ETTINGSHAUSEN – MENÉNDEZ AMOR, 18, pp. 45–46, pl. 16, fig. 2.

1996a *Tsuga moenana* KIRCHHEIMER – BARRÓN, pp. 91–92, text-fig. 15, pl. 7, fig. 3.

Material: MGBV-9467, 9469–9471, 9482, 10366; MGM-48M; MNCNV-3089, 3092, 4743, 4749, 4765–4767, 4774, 4783; MGSB-69390. Specimens collected from the Barranc de Salanca, Coll de Saig and Pedra outcrops.

Description: Cones symmetrical, more or less elliptical, cylindrical or ovoid-elliptical, 18.5–40 (54) mm long, 12–26 mm wide; short peduncle, 2–5 mm long, only preserved in some specimens (e.g., MGBV-9471). Cones formed by 20–30? broadly ovate to orbicular seed scales, 9.6–17.7 mm long and 12.1–19.5 mm wide, with margin entire and apex rounded or cuneate; neither bract scales nor seeds observed.

Discussion: Differentiating between *Tsuga* and *Cathaya* fossil cones can be difficult since many morphological characteristics including the shape of the bract scales and the length and width of the cones are similar (FARJON 1990). Good preservation of the bract scale complex is necessary for any reliable diag-

nosis to be made (FRANKIS 1988, FARJON 1990, LEPAGE 2003); the present lack of seeds as well as bracts makes identifications of these specimens very difficult indeed. However, one feature tentatively might relate the samples from the basin with the genus *Tsuga*. The length/width ratio is closer to that seen for *Tsuga* than for *Cathaya*. The ratios for the present samples are near 1:1, much closer to that generally recorded for *Tsuga* (FARJON 1990). On the other hand, the large number of seed scales (more than 20 in all samples) could also be a valid feature for the comparison between *Tsuga* and *Cathaya*. Certainly, the extant species *C. argyrophylla* CHUN & KUANG and the fossil species *C. vanderburghii* GOSSMANN have fewer than 20 scales (FARJON 1990, MAI 1994, KUNZMANN & MAI 2005). However, the fossil species *Cathaya bergeri* KIRCHHEIMER shows an average of 17–30 seed scales per cone (KUNZMANN & MAI 1995), which it has to be taken into account for the comparison. Because of that, the number of seed scales per strobili seems not to be a conclusive characteristic to differenciate *Cathaya* and *Tsuga*. All in all, we tentatively relate our samples to the genus *Tsuga*.

Interpreting the phylogeny and biogeographic history of *Tsuga* has been difficult given the high phenotypic overlap of features and the lack of significant distinguishing features between species (LEPAGE 2003). The Oligocene and Neogene species *Tsuga schmidtiana* MAI, *Tsuga moenana* KIRCHHEIMER and *Tsuga europaea* MENZEL, differ from the studied specimens by their smaller cones (both in length and width). In addition, *T. schmidtiana* cones have no peduncle and *T. europaea* cones are ovoid (KUNZMANN & MAI 2005). *T. moenana* has cones with an ellipsoid-ovoid shape, 21–37 mm long, 12–17 mm wide; it is probably the fossil species most similar to the studied specimens. The size of the studied cones resembles that of extant North American *Tsuga mertensiana* (BONG.) CARR. cones, which can be up to 8 cm long; they also have a large number (50–80) of cone scales (FARJON 1990). The fossil specimens are also reminiscent of the extant North American species *T. caroliniana* ENGELM. which has similar cones (though a little smaller – only up to 40 mm long) and cone scales similar in shape and number (20–25). The most similar extant species in terms of scale size is *Tsuga dumosa* (D. DON) EICHLER from the Himalayas, which has broadly ovate scales (FARJON 1990).

Pinaceae gen. et sp. indet.

Pl. 1, Fig. 8

1996a Abietoideae tipo 2 – BARRÓN, p. 94, text-fig. 17, pl. 6, fig. 7.

Material: MNCNV-4743. Specimen collected from the Barranc de Salanca outcrop.

Description: Seed scale wide obovate, up to 20.3 mm long and 19 mm wide; margin entire; apex convex or rounded; base not visible; surface longitudinally striated. This seed scale seems to be attached to a poorly preserved bract scale-like structure 1.3 mm long and 0.4 mm wide, and with a slightly dentate-acuminate apex.

Remarks: Differentiating between certain genera of the Pinaceae family – such as *Abies*, *Picea* DIETR., *Tsuga*, *Cathaya* CHUN & KUANG or *Keteleeria* CARR. – on the basis of seed scale morphology is difficult. Indeed, the lack of a well-preserved scale base and bract in the studied specimen impedes any reasonable comparison. This specimen is similar in shape to the seed scales of *Tsuga* and *Cathaya*, although it is longer and wider than those of the extant and fossil species of both genera (FARJON 1990). It also shows some similarities in shape and size to the cone scales of *Abies*, *Picea* and *Keteleeria*. No reliable assignment of the La Cerdanya specimen to a single conifer genus is possible.

Araliaceae JUSS. 1789

Hedera L. 1753a

Hedera cf. *multinervis* KOLAKOVSKII in KOLAKOVSKII & SHAKRYL 1978

Pl. 2, Fig. 1

1978 *Hedera multinervis* KOLAKOVSKII in KOLAKOVSKII & SHAKRYL, p. 141, pl. 3, figs 4–6.

Material: MGSB-69146. Specimen collected at the Pedra outcrop.

Description: Leaf elliptical asymmetric, 7.1 cm long and 3.4 cm wide; apex attenuate; base broken, possibly decurrent; margin entire, irregularly undulate; petiole absent. Midvein straight and moderate; venation suprabasal actinodromous with five primary veins (sub-tripliveined?); secondary venation festooned brochidodromous with 5–6 uniformly curved pairs of secondary veins emerging at 20–25°; intersecondary veins weak; marginal ultimate venation looped; third and fourth order veins random reticulate.

Remarks: This specimen shows clear similarities in shape, size and number of primary veins to the fossil species *Hedera multinervis*, a Miocene taxon described for Abkhazia (Georgia) and Vegora (Greece) (KOLAKOVSKII & SHAKRYL 1978, KVAČEK et al. 2002). Unfortunately, the base of the studied specimen is broken, so it cannot be confirmed that the venation is truly sub-tripliveined, a feature shown by the aforementioned species. Similar leaves from the Messinian of the Gessoso Solfifera Formation (Italy) have been described as *Hedera* cf. *helix* L. (MARTINETTO et al. 2007). The La Cerdanya Basin specimen shows some resemblance to the fertile branch leaves of the extant ivy species *H. helix*. However, the similarities between *H. helix* and other species belonging to this genus, e.g., the other extant Iberian ivy *H. hibernica* (KIRCHN) BEANA (VALCÁRCEL & VARGAS 2003), prevent the association of the specimen with any particular species.

Berberidaceae Juss. 1789

Mahonia NUTT. 1818

Mahonia cf. *pseudosimplex* KVAČEK & WALTHER 2004

Pl. 2, Fig. 2

2004 *Mahonia pseudosimplex* KVAČEK & WALTHER, pp. 31–32, text-fig. 12.4, pl. 14, figs 5–6.

Material: MGBV-9712. Specimen collected from the Prats outcrop.

Description: Leaflet sessile, lamina ovate to lanceolate, slightly asymmetrical, 2.4 cm long and 1.45 cm wide; apical zone not preserved; base subcordate; margin coarsely simple serrate; teeth large, spiny, possibly more than 5 per side, 1–2 mm long; sinus rounded. Midrib straight and stout; venation pinnate semicraspedodromous ending in the tooth apex; secondary venation abruptly curved with more than four veins arising from the midvein at 40–60°, looping and forming inner narrow loops along the midvein; vein angle decreases toward the base; third order veins regular polygonal reticulate; marginal ultimate venation looped.

Discussion: This is the first record of *Mahonia* for the late Miocene of the La Cerdanya Basin. The shape and margin of the studied specimen are very reminiscent of those of the species *M. pseudosimplex* KVAČEK & WALTHER. Both species have an ovate-oblong shape, and have small blades with small lobes. The number of teeth may also be quite similar. The lack of any easily visible venation in *M. pseudosimplex*, however, does not allow for any more accurate comparison. According to KVAČEK & WALTHER (2004), *M. pseudosimplex* is similar to aberrant forms of *M. simplex* ARNOLD from the Palaeogene of North America. However, *M. simplex* has larger lobes and a smaller number of marginal teeth than the La Cerdanya Basin specimen.

M. bilinica (UNGER) KVAČEK & BŮŽEK from the Most Basin differs from the studied specimen in that the former has wider sinuses and conspicuous teeth on its broadly ovate laminas (KVAČEK & BUŽEK 1994). The studied specimen also differs from species of the middle and upper Miocene of eastern Europe, which have densely-toothed leaflets, e.g., *M. kryshtofovichii* STEPHYTRZA, *M. spinulosa* KOLAKOVSKI and *M. heterophylla* KOLAKOVSKI (HABLY et al. 2000, GÜNER & DENK 2012). The present fossil shows clear differences with respect to *Mahonia* (?) *aspera* (UNGER) KOVAR-EDER & KVAČEK, which has leaflets with a basal, acrodromous venation, a petiole, and an irregular, spiny margin. *Mahonia* sp. from the lower Pannonian of Romania also has a petiole, and the lamina is obovate with a margin showing very small teeth (GIVULESCU 1998). *Mahonia* sp. from the early Miocene of Ipolytarnóc (Hungary) does not show elongated, spiny teeth either (HABLY 1985).

Although the fragmentary nature of the studied specimen, as well as the lack of cuticle, makes it difficult to relate it to any single species of barberry, the venation features attribute it to the group Occidentales which now inhabits the New World (AHRENDT 1961, GÜNER & DENK 2012). In fact, its semicraspedodromous venation renders it comparable to the extant North American species *Mahonia aquifolium* (PURSH.) NUTT. and *M. fascicularis* DC.

A misidentification of a leaf of *Quercus drymeja* UNGER (BARRÓN 1996a, BARRÓN 1998; specimen MNCNV-336) as *Mahonia malheurensis* ARNOLD by MENÉNDEZ AMOR (1955: 119–120, pl. 29, fig. 1) has been erroneously taken as valid by several authors (KOVAR-EDER et al. 2006, GÜNER & DENK 2012), and it is corrected herein again.

Betulaceae GRAY 1821

Alnus MILL. 1754

Alnus occidentalis RÉROLLE emend.

Pl. 2, Figs 3–5

1884b *Alnus occidentalis* RÉROLLE, pp. 252–256, pl. 4, figs 4–7.

1884b *Quercus denticulata* RÉROLLE, pp. 267–268, pl. 9, fig. 4.
1945 *Alnus* cf. *kefersteinii* (GOEPPERT) UNGER– VILLALTA & CRUSAFONT, pp. 334, 347.
1955 *Alnus kefersteinii* (GOEPPERT) UNGER– MENÉNDEZ AMOR, pp. 67–68, pl. 21, figs 2–4.
1955 *Alnus occidentalis* RÉROLLE – MENÉNDEZ AMOR, pp. 68–69, pl. 22, figs 1–6.
1955 *Alnus prisca* SAPORTA – MENÉNDEZ AMOR, pp. 69–70, pl. 23, figs 1–2.
1955 *Cotoneaster* sp. – MENÉNDEZ AMOR, pp. 122–123, pl. 46, fig. 7.
1955 *Populus mutabilis* HEER – MENÉNDEZ AMOR, pp. 92–93, pl. 29, fig. 6.
1955 *Populus primigenia* SAPORTA – MENÉNDEZ AMOR, pp. 93–94, pl. 29, fig. 4.
1955 *Quercus denticulata* RÉROLLE – MENÉNDEZ AMOR, p. 78.
1955 *Zanthoxylon juglandinum* BRAUN– MENÉNDEZ AMOR, pp. 143–144, pl. 45, fig. 5.
1996a *Alnus occidentalis* RÉROLLE – BARRÓN, pp. 195–202, text-figs 38–39, pl. 14, figs 6–7, 11–12.
1996c *Alnus occidentalis* RÉROLLE – BARRÓN, pp. 176–181, figs 3 – 6, pl. 1, figs 1–2, 5–6, 8.

Neotype: Specimen MGBV-9492 from the J.F. VILLALTA collection, selected herein, held at the Natural History Museum of Barcelona (NAT) (Pl. 2, Fig. 3).

Occurrence: Coll de Saig outcrop (42° 22' 2"N, 1° 49' 20"W), in the ditches of local road 1411, which runs through a diatomite bed.

Other material examined: MGB-42732–42739; MGBV-9010, 9455, 9495, 9686, 9690, 9696, 9713, 9716, 9720–9721, 9723, 9733, 9737, 9745, 9769, 9771, 9775, 9778, 9787, 9792, 9797, 9800, 9806–9807, 9809–9810, 9872, 9884, 10034, 10038, 10056–10059, 10062, 10068, 10077–10078, 10080–10081, 10083, 10085, 10105, 10141, 10143, 10165, 10491, 10501–10503, 10507, 10509, 10521, 10528, 10556–10557, 10568; MGM-455M, 351M, 421M, 438M, 445M, 453M, 479M, 491M, 493M–496M, 499M, 806M, 974M, 1039M, 1053M–1056M; MGSB-4036, 21770, 31195–31196, 31385, 36197, 40402, 40405, 40412, 40429, 40435, 48113, 48115–48116, 48136–48137, 48139–48142, 48144, 48164; MNCNV-254, 284, 307, 315, 318, 325–326, 328, 335, 339, 348, 358, 367, 704, 708, 735, 737, 739, 746, 764, 768, 779, 828–830, 841, 858, 880, 898, 918, 947, 954, 970, 994, 1002, 3028, 3094, 3558–3560, 3565, 3577, 3580, 3587–3590, 3592, 3595, 3597, 3601–3603, 3613, 3625, 3627, 3634, 3638–3639, 3656, 3661, 3684, 4250, 4342, 4344–4349, 4354–4361, 4365–4375, 4377–4381, 4383–4384, 4386–4393, 4395–4398, 4400–4402, 4411, 4428, 4447, 4603, 4707, 4749, 4836, 4841–4853, 4855–4857. These fossils were collected from all the mentioned outcrops of the La Cerdanya Basin (Text-fig. 1).

Original diagnosis: A. Foliis sæpius longe et gracile petiolatis, polymorphis, elliptic-oblongis v. suborbicularibus, basi rarius subcordatis v. cordatis, margine tenuiter denticulatis; nervis secundariis utrinque 8-10, plus minus curvatis, furcatis v. breviter ramosis; strobilis oblongis, squamis crassis, pedunculis longis robustique.

Emended diagnosis: Leaves symmetrical, elliptical to orbicular; apex convex, acuminate or retuse; base cuneate, convex or rounded; margin serrate; teeth acute sometimes compound, mainly located in the two upper thirds; petiole straight; venation pinnate semicraspedodromous; third order veins percurrent.

Description: Leaves symmetrical, elliptical (Pl. 2, Fig. 3) to orbicular (Pl. 2, Fig. 4), rarely obovate, 1.3–7.4 cm long and 0.9–4.2 cm wide; apex shape convex, acuminate (Pl. 2, Fig. 3) or retuse (Pl. 2, Fig. 5); base cuneate, convex or rounded; margin serrate; teeth acute, sharply pointed, sometimes compound (i.e., with second order teeth), mainly located on the upper two thirds of the lamina; irregular tooth spacing; sinuses acute; petiole straight, up to 3 cm long, rarely completely preserved. Venation pinnate semicraspedodromous, rarely craspedodromous; midrib straight showing moderate thickness; secondary venation uniformly curved with 4–6 pairs of secondary veins emerging at 45–80°; sometimes some secondaries bifurcate near the margin; secondary vein spacing uniform; vein angle increases gradually towards the base; third order veins alternate percurrent; fourth order veins polygonal reticulate; areoles well developed; marginal ultimate tertiary venation looped; loops run parallel to the leaf margin not forming fimbrial veins; sometimes loops ramify threading second order teeth.

Discussion: Observations of the leaf shape, margin and venation of the new material led to an emended diagnosis. The four leaf specimens figured by RÉROLLE (1884b: pl. 4, figs. 4–6) are elliptical and orbicular. The intention of RÉROLLE was to show the clear heterophyllous nature of the leaves of this alder. RÉROLLE also related some female inflorescences to *A. occidentalis* (RÉROLLE 1884b: pl. 4, fig. 8). However, the lack of specimens showing leaves and inflorescences attached at the same branchlet, as well as the presence of another alder species based on leaves in the late Miocene of La Cerdanya, preclude any confident assignment of RÉROLLE's inflorescences to the aforementioned species.

Fossil species of alder similar to *A. occidentalis* include *Alnus acutidens* BOUL. and *Alnus stenophylla* SAPORTA & MARION from the Piazencian of Thèziers (BOULAY 1890), which were described from fragmentarily preserved specimens. Taking into ac-

count features such as the leaf margin, lamina shape and number of secondary veins, the specimen from Thèziers might be assigned to *A. occidentalis*. The specimen from the Miocene of Abkhazia, described as *Alnus ducalis* (GAUD.) KNOBLOCH (KOLAKOVSKII & SHAKRYL 1978, pp. 142–143, pl. 4, fig. 2), may be related to the La Cerdanya Basin species as well. However, *A. ducalis* is clearly different to *A. occidentalis* since it shows larger laminae, deeply emarginated apices and more secondary veins (KNOBLOCH 1969). Although it is sometimes difficult to distinguish between leaves of *Alnus* and *Betula* (CRANE 1981), the Abkhazian fossil unequivocally belongs to the genus *Alnus* given its wide elliptical shape, emarginated and acuminate apex, blunt teeth, and pinnate semicraspedodromous venation. These features clearly differentiate this specimen from other betulaceous genera (see e. g. CRANE & STOCKEY 1987, HUMMEL 1991, ZASTAWNIAK & WALTHER 1998). Although the leaves of *Alnus sporadum* UNGER and *A. sporadum* var. *phocaensis* SAPORTA from the late Oligocene of the Marseille Basin (SAPORTA 1868) also show elliptical and rounded laminae, they have more pairs of secondary veins (8–12) than *A. occidentalis*. RÉROLLE (1884b) and MENÉNDEZ AMOR (1955) considered *A. occidentalis* to be related to the extant *Alnus cordata* DESF. that is native in southern Italy. Nevertheless, the Italian alder shows wider ovate leaves with regular tooth spacing. Herein *Alnus glutinosa* (L.) GAERTN. subsp. *barbata* (C.A. MEY) YALT is regarded as the most similar extant taxon, although its leaves usually have craspedodromous secondary veins (BARRÓN 1996a, BARRÓN 1996c). It has, however, similar leaf shape and margin. *Alnus glutinosa* subsp. *barbata* has been also related to the Miocene species *Alnus cecropiifolia* (ETT.) BERGER by KVAČEK et al. (2002). However, the larger lamina size of this fossil species, its suborbicular to broadly oval leaf shape, subcordate base, regular marginal serration and mainly craspedodromous venation clearly differentiate it from *A. occidentalis*. Today, *A. glutinosa* subsp. *barbata* inhabits riparian and swampy places in northern Anatolia and northern Iran.

Alnus sp.

Pl. 2, Figs 6–7

Material: MGB-44060. This specimen was collected from the Coll de Saig outcrop.

Description: Complete leaf ovate to broadly elliptical, 6.2 cm long and 3.87 cm wide; apical zone rounded; apex divided with two apical teeth (Pl. 2, Fig. 7); base convex; margin serrate; teeth compounds (Pl. 2, Fig. 7), 1.12–2 mm long; primary teeth broadly triangular; secondary teeth (up to 3) smaller; petiole 1.1 cm long. Midrib moderate and straight; venation pinnate craspedodromous; secondary veins (seven pairs) show a straight course and an acute angle of divergence of about 35–40° which increases gradually towards the base within this range; secondary veins only slightly curved in the upper half of the leaf, finishing directly at the primary teeth; tertiary veins percurrent; quaternary veins polygonal reticulate; marginal ultimate venation looped.

Remarks: The studied specimen differs from *A. occidentalis* by its longer compound teeth, craspedodromous venation, and the large number and generally straight course of its secondary veins. Leaves described as belonging to *Alnus* cf. *subcordata* C.A. MEY. from the Sarmatian of Hungary (ANDREÁNSZKY 1959) and the upper Miocene of Romania (GIVULESCU 1990) show similar features but more pairs of secondary veins. Nowadays, *A. subcordata* inhabits the Caucasus, and has leaves very different to those of the studied specimen, with an acute apex and uniformly curved secondary veins. BOULAY (1892: pl. 2, fig. 3) figured a fragmentary specimen from the Pliocene of Mont-Dore (France) which he described as *Alnus insignis* (GAUD.) BOUL. Its morphology is similar to that of the studied specimen, although it has an ovate shape and 7–8 pairs of secondary veins. *Alnus menzelii* RANIECKA-BOBROWSKA has ovate leaves, double serration, simple craspedodromous leaf venation, and straight-running secondary veins (sometimes curved upwards at the apex), but has an acuminate apex and cordate base (WOROBIEC & LESIACK 1998). Extant *Alnus viridis* (CHAIX) DC. has similar leaves. This shrub (or small tree) is found in mountain ranges and boreal areas of the northern hemisphere, sometimes as a pioneer plant. However, it is difficult to assign the present specimen to any fossil species.

Fabaceae LINDL. 1836

Caesalpinites SAPORTA 1862

Caesalpinites sp.

Pl. 2, Figs 8–9

1955 *Cassia lignitum* UNGER – MENÉNDEZ AMOR, pp. 126–127, pl. 48, fig. 5.

1955 *Leguminosites proserpinae* HEER – MENÉNDEZ AMOR, pp. 133–134, pl. 49, fig. 1, 3.

1955 *Podogonium knorrii* (BRAUN) HEER – MENÉNDEZ AMOR, p. 131, pl. 48, fig. 3.

1955 Dicotiledonea, sp. – MENÉNDEZ AMOR, p. 182, pl. 52, fig. 1.

1996a *Caesalpinia* sp. – BARRÓN, pp. 250–251, text-fig. 51, pl. 19, fig. 1.

Material: MNCNV-270, 305, 337, 349, 352, 498. These specimens were collected from the Barranc de Salanca and Prats outcrops, and at an unknown site named "Can Pilbre" by MENÉNDEZ AMOR (1955).

Description: Leaflets elliptical, 1.8–2.3 cm long and 0.6–1.1 cm wide; apex rounded to retuse; base rounded, petiolule ~1 mm long. Midrib straight and moderate; venation pinnate weak brochidodromous; 4–5 pairs of abruptly curved secondary veins arising at 40–60° from the midvein; tertiary veins polygonal reticulate; marginal ultimate venation looped.

Remarks: The described features relate these specimens to several extant genera of the subfamily Caesalpinoideae: *Cassia* L., *Senna* MILL. and *Caesalpinia* L. (LEWIS et al. 2005). SAPORTA (1862) suggested assigning fossil leaflets that could not be attributed to any particular genus of Caesalpinoideae to the genus *Caesalpinites*. The studied specimens show strong similarities to several fossil and extant species of *Caesalpinia*, as well to species of *Caesalpinites*. In fact, they are very similar to *Caesalpinia falconeri* HEER from the Sarmatian of Oehningen (HEER 1859), and to *Caesalpinites (Copaifera) leptobiifolius* described by SAPORTA (1965) from the Aquitanian of Armissant. They can also be compared with leaves described as *Caesalpinites inaequalis* PALAMAREV & PETKOVA from the Volhynian and Bessarabian of Bulgaria (PALAMAREV et al. 2005). They also show strong similarities in shape and venation to *Caesalpinia macrophylloides* KOLAKOVSKII from the Pliocene of Abkhazia, although this species is notably larger (SHAKRYL 1992). Some fossil leaflets from the Eocene of southeastern North America, related to the genus *Caesalpinia* (HERENDEEN 1992, see specimen IU 15820-8436), also show significant similarity to the La Cerdanya Basin specimens.

Leguminocarpon GOEPPERT 1855

Leguminocarpon sp. 1

Pl. 3, Fig. 1

1996a Fabales indet. tipo 4. Legumbre – BARRÓN, pp. 254–255, text-fig. 54B, pl. 19, fig. 11.

Material: CJQ-013. This specimen was collected from the Coll de Saig outcrop.

Description: Pod unilocular, straight, 4–5 times longer than wide (3.1 cm long and 0.9 cm wide); legume slightly asymmetrical, not twisted, with tapered, sessile base and beaked apex; apex and base uniform in texture; seed chamber externally visible; margin not constricted, except at seed insertion points; fruit wings absent; replum not visible. Rounded to elliptical seed, 3 mm long and 1.5 mm wide; funiculus not visible; epicarp reticulately veined.

Remarks: Several features of this fossil legume are reminiscent of certain genera of the subfamilies Caesalpinioideae (e.g., *Afzelia* SMITH, *Apuleia* VON MARTIUS, *Cynometra* L. or *Englerodendron* HARMS) (see LEWIS et al. 2005) and Faboideae (e.g., *Dalbergia* L.). The fruit shows some analogies with fossil material previously attributed to *Leguminocarpon mecsekense* ANDREÁNSZKY from the Hungarian Karpatian of Magyaregregy (ANDREÁNSZKY 1955), with *Leguminocarpon* type IV described by HABLY (1992) for the Egerian, Karpatian and Sarmatian of Hungary (both the latter are now considered to be *Leguminosites parschlugianus* (UNGER) KOVAR-EDER & KVAČEK (KOVAR-EDER et al. 2004)), and with *Dalbergia derrisaecarpa* KOLAKOVSKII from the Pliocene of Abkhazia (SHAKRYL 1992). In addition, the studied specimen shows similarities to IU 15820-5860 from the Eocene of northeastern North America, which, according to HERENDEEN (1992), is reminiscent of *Caesalpinia*. Although some similarities can be established, the information provided by the La Cerdanya Basin fossil is insufficient to assign it to any particular genus.

Leguminocarpon sp. 2

Pl. 3, Fig. 2

1996a Fabales indet. tipo 5. Legumbre – BARRÓN, p. 255, text-fig. 54C, pl. 19, fig. 7.

Material: CJQ-014. This specimen was collected from the Coll de Saig outcrop.

Description: Pod fragmented, symmetrical, straight, not inflated, 7.5 cm long and 0.4 cm wide; base not preserved, long-tapered at apex; stipe not visible; fruit margin not constricted. Seed chambers externally visible; one series of 10 seeds orbicular to rounded inserted along the long axis of the fruit. Seeds obliquely oriented to pod axis, not angular, asymmetrical, ovate; diameter of seeds ~0.5 cm, neither overlapping nor touching to each other; epicarp with surface texture uniform; funiculus 0.1–0.3 cm long.

Remarks: This fossil legume fruit shows similarities to members of genera belonging to the subfamilies Mimosoideae (e.g., *Acacia* MILL. or *Falcataria* (NIELSEN) BARNEBY & GRIMES) and Faboideae (e.g., *Calpurnia* E. MEY. or *Robinia* L.) (see LEWIS et al. 2005). Although *Robinia* shows the closest resemblance in terms of fruit features (shape, size, seed position and type of margin), it is very difficult to rule out the other mentioned genera. The studied specimen resembles *Leguminocarpon* type II or III described for the Egerian, Karpatian and Sarmatian of Hungary (HABLY 1992), which has been related to the extant genus *Dalbergia* L.

Fabaceae gen. et sp. indet.

Pl. 3, Fig. 3

1945 *Andromeda tremula* HEER – Villalta & Crusafont, p. 346, pl. 7.
1955 *Cassia palaeogea* WEBER– MENÉNDEZ AMOR, pp. 125–126, p. 48, fig. 6.
1955 *Robinia regeli* HEER – MENÉNDEZ AMOR, p. 129, pl. 47, fig. 2.
1996a Fabales indet. tipo 1 – BARRÓN, pp. 252–253, text-fig. 52, pl. 19, fig. 4.
1996a Fabales indet. tipo 2 – BARRÓN, p. 253, text-fig. 53, pl. 19, fig. 2.

Material: MGB-42764; MGBV-9496, 10032; MGM-1084M; MNCNV-334, 499, 4466. All these specimens were collected from the Coll de Saig outcrop.

Description: Leaflets ovate to lanceolate, 2.5–3.6 cm long and 0.9–2.1 cm wide; apex acute (without protruding extension of the midrib) to retuse; base rounded; margin entire; petiolule 1.5–4.5 mm long. Midvein straight and moderate; venation pinnate faint brochidodromous; perhaps up to seven pairs of secondary veins uniformly curved arising at 45–55° from the midvein; high order veins and marginal ultimate venation not preserved.

Remarks: Fossil leaflets of this type are usually assigned to the family Fabaceae. The shape, size and primary and secondary venation are similar to the corresponding features seen in members of the genus *Robinia* (e.g., *Robinia pseudoacacia* L.). However, cuticular analyses are necessary to rule out other genera with certainty. Similar fossil specimens have been classified as "*Cassia*" aff. *hyperborea* UNGER *sensu* HEER from the Burdigalian–Helvetian of Moravia (KNOBLOCH 1969), and *Cassia berenices* UNGER and *Robinia regeli* HEER from the Sarmatian of Oehningen (HEER 1859).

Fagaceae DUMORT. 1829

Quercus L. 1753b

Quercus hispanica RÉROLLE emend.

Pl. 3, Figs 4–5

1884b *Quercus hispanica* RÉROLLE, pp. 268–274, pl. 6, figs 1–11.
1945 *Quercus hispanica* RÉROLLE – Villalta & Crusafont, p. 344, pl. 1.
1947 *Quercus hispanica* RÉROLLE – SOLÉ SABARÍS & LLOPIS LLADÓ, p. 93, pl. 14.
1955 *Myrica vindobonensis* (ETTINGSHAUSEN) HEER – MENÉNDEZ AMOR, p. 88, pl. 20, fig. 2.
1955 *Quercus hispanica* RÉROLLE – MENÉNDEZ AMOR, pp. 80–82, pl. 26, figs 1–4.
1995 *Quercus hispanica* RÉROLLE – ARROYO GARCÍA, p.157, pl. 13, fig. 4.
1996a *Quercus hispanica* RÉROLLE – BARRÓN, pp. 181–187, fig-text. 37, pl. 14, figs 3–4.
1996 *Quercus hispanica* RÉROLLE – DIÉGUEZ et al., pp. 335, 337, pl. 2, figs 2–3.
1998 *Quercus hispanica* RÉROLLE – BARRÓN, pp. 29–32, pl. 2, figs 8–9, pl. 3, figs 1–3.

Neotype: Specimen MGM-1063M (Pl. 3, Fig. 4) of the VILLALTA and CRUSAFONT collection, selected herein, held at the Geomining Museum (IGME).

Occurrence: The Pedra outcrop (42° 20' 41.15"N, 1° 48' 38.62"E) to the NE of Bellver de Cerdanya village, in a diatomitic bed.

Other material examined: MGB-28730, 29357, 29545, s/n1–s/n5, 42541–42561; MGBV-9475, 9511, 9516, 9518, 9708, 9731–9732, 9742, 9766, 9768, 9848, 9879a-b, 9907, 10030, 10033–10034, 10039, 10043, 10051, 10132, 10148, 10152, 10464, 10470–10472, 10474–10475, 10485, 10517, 10523, 10565; MGM-349M, 390M, 439M, 441M–442M, 971M, 1046M, 1062M, 1096M; MGSB-21772, 31015, 31201–31202, 31313, 31322, 31375, 31384, 36191, 40314, 40316, 40404, 40411, 40424, 40426, 40443, 40446, 44390, 45467–45469, 47031, 47034, 47038, 48134, 48155, 48161, 48164, 48170, 48461; MNCNV-276, 327, 376, 378–379, 381, 384–385, 442, 444–451b, 470, 524–527, 529, 531–537, 540–542, 663, 666, 668, 671–672, 678, 683, 728, 774, 847, 946, 2544a, 3017–3021, 3024, 3026–3027, 3029–3030, 3035, 3039–3040, 3048, 3064, 3076–3079, 3082, 3113–3115, 3119, 3133–3138, 3146, 3500, 3506, 3508, 3516–3517, 3523, 3530, 3532–3533, 3535, 3538, 3544, 3554, 3556, 3568, 3680, 3683, 4250–4254, 4259–4260, 4263, 4266, 4272–4278, 4283, 4286–4288, 4291–4292, 4295–4296, 4298, 4304, 4306–4307, 4309–4311, 4314, 4317, 4320, 4322–4325, 4327–4328, 4331–4332, 4341, 4399, 4426, 4436, 4532, 4588, 4606–4607, 4806–4807, 4837–4839, 5044. These fossils were collected from all the mentioned outcrops of the La Cerdanya Basin (Text-fig. 1).

Original diagnosis: Q. foliis firmis vel submembranaceis, sat breviter petiolatis, oblong-ellipticis v. obova-

tis, basi obtusatis v. subauriculatis, v. in petiolum attenuates, apice plus minus longe cuspidatis, margine parce crenato-dentatis v. sublobatis, nervis secundariis 7–10 in dentes productis, nervulis rete subtile efformantibus.

Emended diagnosis: Subcoriaceous leaves mainly obovate, sometimes elliptical or ovate; apex acute sometimes slightly attenuate; base mainly symmetrical, cuneate to rounded; margin lobate on the upper two thirds of the lamina; basal third with entire margin; teeth with acute sinus and mucronate apex; short and straight petiole; pinnate mixed craspedodromous venation; midvein straight and stout; 7–10 pairs of secondary veins opposite and alternate; tertiary veins percurrent.

Description: Leaves mainly obovate, more rarely elliptical or ovate, about 2.5–8.8 cm long and 1.3–3.3 cm wide; apex acute sometimes slightly attenuate, with angle between 40° and 65°; base mainly symmetrical, cuneate to rounded, sometimes slightly cordate; margin lobate in the upper two thirds of the lamina, some specimens sub-lobed; basal third with entire margin; 3–7 pairs of large teeth, around 0.5 cm long and 0.5–0.9 cm wide, slightly curved towards the blade; the teeth have straight to concave apical sides, and convex basal sides; sinus acute; tooth apex acute, sometimes mucronate; short and straight petiole, 2–8 mm long. Pinnate mixed craspedodromous venation; midvein straight and stout; 7–10 pairs of secondary veins opposite and alternate, straight or slightly curved, finishing in a tooth or an abrupt curve; secondary vein spacing uniform; angle of divergence 35–65° increasing gradually towards the base within this range, although secondaries may occasionally emerge at 90° at the base; tertiary veins mixed opposite-alternate percurrent with vein course straight, forming an obtuse angle with the primary vein of about 130–140° increasing exmedially within this range; fourth order venation regular polygonal reticulate, forming a network with well-developed areoles; marginal ultimate venation looped.

Discussion: This oak species is very common in the La Cerdanya Tortonian outcrops but also occurs at other late Miocene and Pliocene sites in southwestern Europe (DEPAPE 1922, TEIXEIRA 1952, GRANGEON 1958, ROIRON 1981, ROIRON 1991). RÉROLLE (1884b) described three varieties of *Q. hispanica* with elliptical (*Q. hispanica genuine*: pl. 6, figs 1–2), acuminate (*Q. hispanica cuspidate*: pl. 6, fig. 5) and obovate leaf shapes (*Q. hispanica expansa*: pl. 6, figs 8–9). However, the heterophyllous character of this species invalidates these varieties, which do not have any taxonomic value nowadays (BARRÓN 1996a, BARRÓN 1998).

Q. hispanica is similar to several southern European extant species belonging to the subgenus *Quercus*, especially *Q. humilis* MILL. (= *Q. pubescens* L.), *Q. faginea* LAM. ssp. *faginea* and *Q. lusitanica* LAM. All of these are now found in the Iberian Peninsula, and their leaves are similar in morphology, shape, size, base and margin to those of *Q. hispanica*. *Q. humilis* is a Submediterranean species which inhabits central and southern Europe and southwest Asia. PALAMAREV (1989) indicates the existence of this species in Poland during the Miocene and Pliocene. *Q. faginea* also has very similar leaf characteristics, especially *Q. faginea* ssp. *faginea*, a very polymorphic species (DO AMARAL FRANCO 1990). This taxon has leaf margins very similar to those seen in some of the La Cerdanya Basin specimens (e.g., MNCNV-4273). Finally, *Q. lusitanica* (= *Q. fruticosa* BROT.), which is widespread in central and southern Portugal, southern Spain and Morocco, has no lobes or teeth at the basal third leaf margin – a feature also seen in the present samples which are of similar size and shape. Some leaves of *Quercus petraea* (MATT.) LIEBL. and *Q. robur* L. show some resemblance to the present specimens. However, they are commonly longer, obovate or oblong-obovate, and have pronounced lobes. Unfortunately, no cuticular studies have been performed on *Q. hispanica* that would allow this species to be related to any other extant or fossil species. Morphologically, it resembles several specimens of *Q. pseudocastanea* GOEPPERT emend. WALTHER & ZASTAWNIAK from the Miocene of Silesia (WALTHER & ZASTAWNIAK 1991). However, this species, which belongs to the section *Cerris* OERSTED, has usually much larger leaves, showing longer laminae (> 10 cm), craspedodromous venation, and teeth in the basal area. *Q. hispanica* was parasitised by Hymenoptera of the genus *Neuroterus*, which produced circular galls between the secondary veins (DIÉGUEZ et al. 1996, pl. 2, figs 2–3).

Quercus sp.

Pl. 3, Fig. 6

1945 *Fraxinus praedicta* HEER – VILLALTA & CRUSAFONT, pp. 351–352, pl. 5.

1992a *Fraxinus excelsior* L. (pars) – BARRÓN, p. 106, pl. 1, figs 7–8.

Material: MGBV-9493; MGSB-69438. These specimens were collected from the Coll de Saig outcrop.

Description: Leaves elliptical, 4.3–5 cm long and 1.7–2.5 cm wide with a sclerophyllous appearance; apex acute; base cuneate; margin simple serrate, entire in the lower part; teeth small and fine, concave to straight on the apical side and straight on the basal side; sinus flat; petiole short, 5–9 mm long. Midrib straight and stout; venation pinnate mixed craspedrodromous; secondary venation straight with 8–13 pairs of secondary veins arising from the midvein at 35–75°; several secondary veins forked near the margin; presence of intersecondaries; third order veins percurrent, sometimes exmedially ramified; marginal ultimate venation looped.

Remarks: The shape, size, type of margin and venation shown by the studied specimens allow to attribute them to the genus *Quercus*. However, assignement to a definite species is more difficult given the foliar polymorphism shown by many species of this genus, and not least the taxonomic difficulties associated with fossil oaks (Kvaček & Walther 2004). The studied specimens share some morphological similarities with *Quercus sosnowskyi* Kolakovskii, a Miocene species that inhabited France, eastern Europe and western Asia from the Miocene to the Pliocene (Palamarev 1989, Palamarev & Tsenov 2004, Kovar-Eder et al. 2006). This species has been related to *Q. suber* L. group by virtue of its epidermal features, leaf shape and cupules (Kvaček et al. 2002). The studied specimens may also be compared to other species belonging to this genus, such as *Q. ilex* L. ssp. *fossilis* (see e.g., Kitanov 1984: pl. 12, fig.1; Palamarev & Tsenov 2004: pl. 1, fig.6).

Lauraceae Juss. 1789

Laurophyllum Goeppert 1857

Laurophyllum sp.

Pl. 3, Fig. 7

1884b *Persea* sp. – Rérolle, pp. 286–288, pl. 10, fig. 4.
1945 *Ficus lanceolata* Heer – Villalta & Crusafont, p. 345, pl. 9.
1955 *Dodonea pteleoefolia* (Weber) Heer– Menéndez Amor, pp. 147–148, pl. 43, fig. 3.
1955 *Ficus lanceolata* Heer – Menéndez Amor, pp. 103–104, pl. 32, fig. 1.
1955 *Quercus salicina* Saporta– Menéndez Amor, p. 85, pl. 27, fig. 1.
1955 *Rhododendron megiston* Unger – Menéndez Amor, p. 163, pl. 38, fig. 6.
1996a *Laurophyllum* sp. – Barrón, pp. 104–107, text-fig. 20–21, pl. 8, fig. 9.

Material: MGB-42678; MGBV-9749, 9803; MGM-109M, 1073M, 1082M; MGSB-31369, 40415, 40437, 44392; MNCNV-258–259, 375, 463–465, 486, 510–512, 517, 520, 793, 850, 894, 905, 2570, 3086, 3585, 3635–3636, 3662–3663, 3670, 4624–4625, 4628, 4632, 4637–4641, 4645–4646, 4703, 4851. These specimens were collected from the Coll de Saig and Beders outcrops.

Description: Leaves elliptical, 4.1–10.2 cm long and 1.1–3.9 cm wide; apex acute to acuminate; base cuneate to rounded; margin entire; petiole 0.2–1.3 cm long. Midrib moderate and straight; venation pinnate brochidodromous; secondary venation uniformly and abruptly curved with 6–8 pairs of secondary veins arising at 45–80°; vein spacing uniform; presence of intersecondary veins; marginal ultimate venation looped; third order veins percurrent with obtuse angle with respect to the midrib; fourth order veins polygonal reticulate.

Remarks: The studied specimens show similar features to the leaves of the extant laurel tree (*Laurus nobilis* L.) of Mediterranean and Macaronesian distribution (Rodríguez-Sánchez et al. 2009). Leaves similar to *Laurus* have usually been recorded for the late Miocene and Pliocene of the western Mediterranean region (Barrón 1996a). Unfortunately, preserved cuticles are essential for identifying fossil leaves of *Laurus* (Ferguson 1974), and none are present in the La Cerdanya Basin specimens. The studied specimens can, therefore, only be assigned to the genus *Laurophyllum*.

cf. *Laurophyllum* sp.

Pl. 3, Fig. 8

1955 *Laurus princeps* Heer – Menéndez Amor, pp. 112–113, pl. 34, fig. 1.
1996a *Persea princeps* (Heer) Schimper – Barrón, pp. 109–113, text-fig. 23, pl. 9, fig. 1.

Material: MNCN-4605, MGB-42782, MGM-227M. All three specimens were collected from the Coll de Saig outcrop.

Description: Leaves elliptical to obovate, 4.2–15.5 cm long and 1.8–4.52 cm wide; apex acute to acuminate; base cuneate; margin entire; petiole not preserved. Midvein straight and stout; venation pinnate weak brochidodromous; secondary venation straight with 12–16 pairs of secondary veins emerging at 30–55°; occasional dichotomies; intersecondary veins usual; marginal ultimate venation with complete loops;

third order veins percurrent; fourth vein category random reticulate.

Remarks: The leaf venation, lamina shape and size relate these specimens to the family Lauraceae. A similar general shape, size, venation and apex are seen in extant species belonging to the genera *Rhodostemonodaphne* NEES, *Aniba* AUBL., *Ocotea* AUBL. and, especially, *Persea* MILL. Indeed, the studied specimens have the same pattern of venation as the recent *Persea cuneata* MEINS of South America. Specimen MNCN-4605 shows some clear similarities in terms of shape and venation to a specimen identified as *Ocotea oblanceolata* PALAMAREV & PETKOVA from the early Sarmatian of Bulgaria (PALAMAREV et al. 2005), while specimen MGB-42782 shows clear similarities to a specimen described as *Persea princeps* (HEER) SCHIMPER from the late Miocene of Romania (GIVULESCU 1990: pl. 7, fig. 4). These specimens can also be compared, in terms of their shape and venation, with extant species belonging to the family Magnoliaceae, such as *Magnolia grandiflora* L. and *M. urraoensis* (LOZANO) GOVAERTS. However, the lack of cuticular features means the La Cerdanya Basin fossils cannot be confidently assigned to any particular family. However, a tentative identification of cf. *Laurophyllum* sp. is proposed.

Lythraceae SAINT-HILAIRE 1805

Decodon J.F. GMELIN 1791

Decodon sp.

Pl. 5, Fig. 8

1945 *Salix tenera* (BRAUN) HEER – VILLALTA & CRUSAFONT, pp. 344, 348, pl. 3.
1955 *Conospermum macrophyllum* ETTINGSHAUSEN – MENÉNDEZ AMOR, p. 108, pl. 33, fig. 6.
1955 Dicotiledónea, sp. – MENÉNDEZ AMOR, p. 179, pl. 50, fig. 1.
1955 Dicotiledónea, sp. – MENÉNDEZ AMOR, p. 181, pl. 51, fig. 2.
1996a *Myrica marginalis* HEER – BARRÓN, pp. 152–154, text-fig. 31, pl. 11, fig. 6.

Material: MGBV-9523; MGM-1086M; MNCNV-361. These specimens were collected from the Coll de Saig and Beders outcrops.

Description: Leaves, lanceolate to oblanceolate, 4.3–5 cm long and 1.1–3 cm wide; apex acute; base cuneate; margin entire; petiole stout 2–6 mm long. Venation pinnate brochidodromous; secondaries seem to end in a poorly preserved vein paralleling the leaf margin; midvein stout and straight; secondary venation abruptly curved, alternate or sub-opposite with more than 18 pairs of secondary veins arising at 75–90°; intersecondaries abundant; tertiary venation polygonal reticulate; marginal ultimate venation looped.

Remarks: These leaves have been related to several families of dicotyledons, such as Moraceae, Apocynaceae incl. Asclepiadaceae, and Myrtaceae (KVAČECK & SAKALA 1999). In fact, the studied specimens themselves have been previously assigned to different genera such as *Conospermum* SM., *Myrica* L. and *Salix* L. However, they differ by the presence of dense venation and an obtuse-to-90° vein divergence. In addition, the lack of fimbrial veins rules out comparison with the family Apocynaceae. The present specimens have also been compared to the Portuguese Miocene fossil species *Myrica marginalis* HEER (HEER 1881), although TEIXEIRA & PAIS (1976) considered this species to be invalid. When all the morphological features are taken into account, the specimens are reminiscent of the genus *Decodon*. Certainly, they match well: both the studied specimens and *Decodon* have elliptical to lanceolate leaves, decurrent bases, an acute apex, a prominent midvein and a stout petiole. The brochidodromous dense venation is also shared. All these features can be observed in the fossil species *Decodon gibbosus* (E.M. REID) E.M. REID in NIKITIN (KVAČECK & SAKALA 1999). Nevertheless, *D. gibbosus* (which includes material previously described as *Ficus multinervis* HEER and *Apocynophyllum helveticum* HEER) has wider and longer leaf blades, and petioles that are much longer than those of the studied specimens. In addition, *Decodon gibbosus* clearly shows a distinct intramarginal vein while in the studied specimens it is much less obvious. *Decodon alaskanus* WOLFE & TANAI has wider and more elliptical leaves (WOLFE & TANAI 1980). The state of preservation of the studied fossils (and their fragmentary nature) allows for no further comparison. Moreover, the lack of any epidermal preservation or clear phyllotaxy renders it impossible to assign them to any particular species.

Malvaceae Juss. 1789

Tilia L. 1753a

Tilia vidali RÉROLLE emend.

Pl. 3, Figs 9–10; Pl. 4, Figs 1–3

1884b *Tilia vidali* RÉROLLE, pp. 293–296, pl. 10, fig. 11, pl. 11, figs 1–2.
1955 *Ficus tiliaefolia* BRAUN – MENÉNDEZ AMOR, pp. 102–103, pl. 32, fig. 4.

1955 Tilia vidali RÉROLLE – MENÉNDEZ AMOR, pp. 141–142, pl. 39, figs 3–4.
1955 *Viburnum ceretanum* MENÉNDEZ AMOR, pp. 172–174, pl. 35, fig. 5.
1955 *Viburnum tiliaeoides* WARDA – MENÉNDEZ AMOR, p. 174, pl. 35, fig. 6.
1996a *Tilia vidali* RÉROLLE – BARRÓN, pp. 225–229, text-figs 46–47, pl. 17, figs 3–4.

Neotype: Specimen MNCNV-288 from the J. MENÉNDEZ AMOR collection, selected herein, held at the National Museum of Natural History (CSIC) (Pl. 3, Fig. 9).

Occurrence: Coll de Saig outcrop (42° 22′ 2″N, 1° 49′ 20″W), in the ditches of local road 1411, which runs through a diatomite bed.

Other material examined: MGB-42740; MGBV-10139; MGSB-31224; MNCNV-245, 262, 346, 355, 753–754, 4704–4707, 4829. These specimens were collected from the Barranc de Salanca, Coll de Saig and Beders outcrops.

Original diagnosis: T. foliis late ovatis, ad basim valde cordatis, apice breviter acuteque acuminates, quandoque sublobatis, margine grosse denticulatis, nervis primariis 5–7, nervo medio penninervio, n. primariis lateralibus exlus ramosis, nervulis plerumque simplicibus transversim decurrentibus; fructu bracteam majusculam, lingulatam, basi rotundatam, pedicellosque prope capsulas inflatos præbente.

Emended diagnosis: Ovate leaves, sometimes subtrilobed; apex acute to acuminate; base cordate; margin serrate; teeth acute, sometimes compound; petiole straight; venation actinodromous basal with 3–5 primary veins; secondary venation craspedodromous; tertiary venation percurrent; cuticle with isodiametric cells; stomata anomocytic. Bracts leaf-like oblong; apex rounded; base cuneate, convex or rounded; margin entire; peduncle short and straight; venation pinnate festooned brochidodromous; third and fourth order venations polygonal reticulate.

Description: Leaves ovate, sometimes subtrilobed, 7–10 cm long and 4.5–12 cm wide; lamina sometimes asymmetrical; apex acute to acuminate; base cordate; margin serrate; teeth acute, mucronate, sometimes compound with second order teeth (Pl. 3, Figs 9–10); teeth flexuous on the apical side and convex on the basal side; sinus acute; tooth spacing irregular; petiole up to 4 cm long, rarely completely preserved. Venation actinodromous basal with 3–5 primary veins (Pl. 3, Fig. 9); midrib stout and straight; rest of primaries straight and moderate; secondary venation craspedodromous with 5–6 uniformly curved pairs of secondaries emerging at 30–35°; secondary vein spacing increasing towards the base; presence of compound agrophic veins; third order veins mixed opposite-alternate percurrent, with vein angle increasing exmedially; fourth order venation regular polygonal reticulate; marginal ultimate venation looped. Poorly preserved abaxial epidermal compression (Pl. 4, Fig. 1) shows isodiametric cells 7.5–15 μm in diameter; epidermal cells longer and polygonal on the veins, 22.4–45 μm long and 6–10.4 μm wide; anomocytic stomata, 41.6–45.8 μm long and 22.3–30 μm wide, occur randomly in the areoles. A fragmentary xylematic structure 60 μm long and 4–5 μm wide can be seen (probably a group of interconnected vessels) on the leaf surface (Pl. 4, Fig. 2); circular pit-like structures appear along the length of the mentioned xylem remains.

The associated bracts are leaf-like, oblong in shape, 4.6–6.5 cm long and 1.2–1.5 cm wide (Pl. 4, Fig. 3); apex rounded; base cuneate, convex or rounded; margin entire; peduncle ~0.5 mm long. Primary vein stout; secondary venation abruptly curved with 10 pairs of secondary veins emerging at 30–90°; venation pinnate festooned brochidodromous; occasional intersecondary veins; third and fourth order venations polygonal reticulate; marginal ultimate venation looped.

Discussion: The studied leaf remains are reminiscent of the late Miocene species *Tilia waltheri* GIVULESCU and *Tilia* sp. 2 from Chiuzbaia (Romania) (GIVULESCU 1979, GIVULESCU 1990). *T. waltheri* leaves are similar in size and venation to those of *T. vidali*, but the former species has compound marginal teeth with large secondary teeth while the latter has shorter secondary teeth. The leaves of the middle Miocene northern species *Tilia selardense* GRÍMSSON, DENK & SÍMONARSON are slightly larger. In addition, they have deeply cordate to near-auriculate bases, and a smaller number of primary veins (GRÍMSSON et al. 2007). The early Miocene *Tilia brabenecii* BŮŽEK & KVAČEK also shows similar morphological features, although it has a sharply aristate-dentate margin (BŮŽEK & KVAČEK 1992). The leaves of the Oligocene species *Tilia gigantea* ETTINGSHAUSEN differ from those of the La Cerdanya Basin by their slightly trilobate shape, cordate to truncate bases, numerous secondaries and serrate margin (KVAČEK et al. 2004). RÉROLLE (1884b: pl. 10, fig. 11) described a bract with a cluster of two fruits attached at the end of a peduncle inserted in the middle part of the primary vein of the bract. However, no fossil like this was found by the present authors, either during fieldwork or in any museum collection. On the other hand, after more than a century of stud-

ies in the basin any researcher or amateur has found other kind of bract or leaf related to *Tilia* species. For this reason, we tentatively include these macroremains in the species *T. vidali*, though leaves and bracts do not appear in anatomical connection. Other authors have used the same criterion to relate specimens without anatomical connection, for example, the case of the fruits and leaves of *Buxus pliocenica* SAPORTA & MARION from the Pliocene of Meximieux (SAPORTA & MARION 1876, KVAČEK et al. 1982).

The bracts of *T. vidali* are of similar size and venation to other European fossil species of linden, e.g., *Tilia longibracteata* ANDR., *T. megacarpa* GIVULESCU & OLOS, *T. branbenecii* BŮŽEK & KVAČEK and *T. atavia* SPITZLBERGER, which formed a group of widespread species in central and eastern Europe during the Miocene (KNOBLOCH 1969, GIVULESCU & OLOS 1973, SPITZLBERGER 1984, BŮŽEK & KVAČEK 1992, KNOBLOCH & KVAČEK 1996). These species have the floral peduncle fused to the extreme base of the bract lamina – which relates them to the type B lindens of MANCHESTER (1994) – a type of bract that can be traced from the early Miocene to the Pliocene in western and central Europe. RÉROLLE (1884b: pl. 10, fig. 11) described and recorded a bract for a specimen collected in the La Cerdanya Basin showing the peduncle fused medially along the basal third of the bract. This bract-peduncle structure was denoted type C by MANCHESTER (1994), and according to this author characterises all the extant taxa in North America and Europe and most of the extant species of Asia; it was unknown prior to the late Pliocene in Europe. However, the type C bract-peduncle structure is also shown by the Romanian late Miocene *Tilia ovoidea* GIVULESCU & OLOS (1973: pl. 21, fig. 11). The occurrence of *T. ovoidea* and *T. vidali* demonstrates the presence of Manchester's type C linden for the late Miocene in Europe. Given its leaf and bract morphology, *T. vidali* can be compared with the extant *Tilia americana* L. from eastern North America, and *Tilia rubra* DC. from the Carpathians. Several leaves of the large-leaved lime (*Tilia platyphyllos* SCOP.) are also similar to some of the studied specimens.

Meliaceae Juss. 1789

Cedrela P. BROWNE 1756

Cedrela heliconia (UNGER 1850) KNOBLOCH 1998

Pl. 4, Fig. 4

1850 Sapindus heliconius UNGER, p. 457.

1884b *Fraxinus* sp. (pars) – RÉROLLE, pp. 291–293, pl. 10, fig. 10.

1955 *Juglans acuminata* BRAUN – MENÉNDEZ AMOR, pp. 88–89, pl. 44, fig. 1.

1996a aff. *Cedrela* sp. – BARRÓN, pp. 293–294, text-fig. 62, pl. 22, fig. 9.

1998 *Cedrela heliconia* (UNGER) KNOBLOCH, p. 69, text-fig. 29a–b, pl. 47, figs 1, 6.

Material: MGBV-9783, 10044, 10560; MNCNV-4460, 4792; BC-1115. These specimens were collected from the Barranc de Salanca, Torrent de Vilella and Coll de Saig outcrops.

Description: Leaflets lanceolate rarely ovate (e.g., specimen MGBV-9783), moderately asymmetrical, 2.63–9.14 cm long and 1.23–2.1 cm wide; apex acuminate; base convex to rounded; margin entire; petiolule short ~1.3 mm long. Venation pinnate brochidodromous; secondary venation abruptly curved with 8–18 pairs of secondary veins emerging at 60–90°; secondary vein angle increases gradually towards the base; few intersecondary veins present; third order veins percurrent; fourth order veins polygonal reticulate; marginal ultimate venation looped.

Discussion: Although KNOBLOCH (1998) proposed the new combination *C. heliconia*, he indicated that the foliage associated with this species could also be seen in the genus *Sapindus*. Indeed, according to ZASTAWNIAK (1980), the morphological features of the leaves of the genera *Cedrela*, *Juglans* and *Sapindus* show strong similarities. However, *Juglans* leaflets are distinguishable by their more regular parallel arrangement of the secondary veins, the intersecondaries being absent or very scarce. The leaflets of the genus *Sapindus*, however, have numerous and well developed intersecondary veins. In *Cedrela*, the leaflets have relatively few and little distinct intersecondaries. This is also true for the present specimens and, consequently, they are attributed to *Cedrela*.

Specimens belonging to the tribe *Cedreleae* (genera *Cedrela* and *Toona* [ENDL.] M. ROEM.) have been recorded in Europe from the Eocene to the Pliocene (FERGUSON & KNOBLOCH 1998, MUELLNER et al. 2010), with the genus *Cedrela* widely recorded for central and eastern Europe (UNGER 1850, KOVÁCS 1957, PALAMAREV & PETKOVA 1987, AMBERT & ROIRON 1990, ROIRON 1991, KNOBLOCH 1998; FERGUSON & KNOBLOCH 1998, IAMANDEI et al. 2005). The La Cerdanya Basin specimens are very similar in shape to those of the Messinian of Murviel-Les-Beziers (France) described by AMBERT & ROIRON (1990) as *Cedrela* sp. Although KNOBLOCH (1998)

stated that *Cedrela* was not a thermophilous element, the nearest living relatives of *C. heliconia* are several tropical and subtropical species of the genera *Cedrela* and *Melia* L. (THIEL et al. 2012). Some resemblances with leaflets of the extant *Toona sinensis* (A. JUSS.) M. ROEMER from East Asia and *Toona ciliata* M. ROEMER from Australia can also be seen. Although this is the first citation of *Cedrela* for the La Cerdanya Basin, pollen of the family Meliaceae has been recorded here (BESSEDIK 1985). This genus, however, has not previously been cited as part of the Iberian fossil record (POSTIGO-MIJARRA et al. 2009).

Myricaceae RICH. ex KUNTH 1817

Myrica L. 1753b

cf. *Myrica* sp.

Pl. 4, Fig. 5

1884b *Quercus weberi* HEER – RÉROLLE, pp. 275–276, pl. 9, figs 6–7.
1955 *Berberis rhopaloides* SAPORTA – MENÉNDEZ AMOR, pp. 120–121, pl. 39, fig. 2.
1955 *Callicoma microphylla* ETTINGSHAUSEN – MENÉNDEZ AMOR, p. 121, pl. 38, fig. 5.
1955 *Fraxinus gracilis* SAPORTA – MENÉNDEZ AMOR, pp. 170–111, pl. 36, fig. 1.
1955 *Quercus weberi* HEER – MENÉNDEZ AMOR, p. 86.
1996a *Myrica lignitum* (UNGER) SAPORTA – BARRÓN, pp. 148–152, text-fig. 31, pl. 11, fig. 6.

Material: MNCNV-265, 267, 272, 277–278, 282, 469, 472–473, 478–480, 495, 497–498, 504, 530, 538–539, 835, 4558. These fossils were collected from the Barranc de Salanca, Coll de Saig and Balltarga outcrops.

Description: Leaves elliptical to narrow elliptical, 1.6–6 cm long and 0.5–1.7 cm wide, usually poorly preserved; apex acute; base symmetrical, rounded to cuneate; margin simple serrate; teeth small and fine; teeth straight to flexuous on the apical side and retroflexed on the basal side; tooth apex acute, sometimes rounded; sinus acute; basal area with entire margin; petiole straight 1–7.5 mm long. Midrib moderate and straight; venation pinnate craspedodromous to semicraspedodromous; secondary venation straight with 9–16 pairs of secondary veins arising at 45–80°; vein spacing uniform; secondary vein angle increasing gradually towards the base; occasional intersecondaries; third order veins random reticulate to alternate percurrent; marginal ultimate venation looped.

Remarks: RÉROLLE (1884b) and MENÉNDEZ AMOR (1955) previously attributed the present specimens to the genera *Berberis* L., *Callicoma* ANDREWS, *Fraxinus* L. and *Quercus* L., although these are clearly different since they do not have marginal, straight to flexuous teeth on the apical side or retroflexed teeth on the basal side. Different species of *Myrica* show such marginal teeth, but this genus usually has semicraspedodromous leaves – a feature only seen in a few of the studied specimens. In addition, the tertiary venation is generally random reticulate in *Myrica*, but partially alternate percurrent in some of the fossil specimens. The lack of cuticles precludes any accurate identification.

Due to its very similar shape, margin and venation, the North American late Eocene *Myrica zacharensis* LESQ. (BERRY, 1924) is the fossil species most similar to the La Cerdanya Basin specimens. *Myrica linearis* SAP. and *Myrica sagoriana* ETT. also show similarities in terms of the marginal serration of the leaves (SAPORTA 1862, KNOBLOCH & KVAČEK 1981). The studied species may be compared to the extant *Myrica arborea* HUTCH., from Equatorial Guinea, although the latter usually has wider laminae with clearly random reticulate tertiary venation.

Rhamnaceae JUSS. 1789

Rhamnaceae gen. et sp. indet.

Pl. 4, Fig. 6

1996a *Cornus* sp. – BARRÓN, pp. 265–266, text-fig. 56, pl. 20, fig. 6.

Material: MNCNV-263, 4701. These specimens were collected from the Coll de Saig outcrop.

Description: Leaves elliptical, 2.6 cm long and 1.4 cm wide; apex acute; base convex and slightly asymmetrical; margin entire and undulate; petiole 0.2 cm long. Midvein moderate and straight; venation pinnate eucamptodromous; secondary venation uniformly curved with seven subopposite pairs of secondary veins arising from the midvein at 45°; secondary vein angle increases gradually towards the base; third vein category percurrent; third vein angle to midvein obtuse; fourth order veins polygonal reticulate; marginal ultimate venation looped.

Discussion: The features of the margin and venation relate the studied specimens to different species of the rhamnaceous genera *Berchemia* NECK. ex DC., *Rhamnus* L. and *Frangula* MILL. The former genus is today composed of 12 species of small trees or climbers native to Africa, Asia and America (RICHARDSON et al. 2012). Its fossils are common in Oligocene and Miocene assemblages of central Europe (see HEER

1859, Hably 2006, Kvaček & Teodoridis 2007). This genus has been identified in sediments from the early Miocene of Spain (Barrón 1999). Recently, Kovar-Eder et al. (2004) indicated that the foliar morphology of the fossil species accommodated in the genus *Berchemia* occurs in different genera of the family Rhamnaceae. The most important of these genera is *Rhamnus*, with about 125 species widely distributed across the northern hemisphere to Brazil and South Africa (Richardson et al. 2012). The studied specimen resembles *Rhamnus graeffii* Heer from the Miocene of Oehningen (Heer 1859: 79, pl. 126, fig. 4), although the latter species has a percurrent tertiary vein almost perpendicular to the midvein. Some specimens of *Rhamnus rectinervis* Heer also show features similar to those of the studied specimens. However, they have more than 10 pairs of secondary veins (Heer 1859: 80, pl. 126, figs 2–6; Palamarev & Bozukov 2004: pl. 4, fig. 4). The specimen identified as *Rhamnus gaudinii* Heer from the Miocene of Romania (Givulescu & Olos 1973: 20–21, pl. 4, fig. 6) also resembles the studied specimen in terms of its shape and venation, although this species has serrated leaf margins. The specimen from the Oligocene Cervera Basin, identified as *Rhamnus aizoon* Unger (Sanz de Siria 1992), also shows some clear similarities with the present specimens in terms of shape, size and venation. Nevertheless, certain species attributed to *Rhamnus* (e.g., *Rh. gaudinii* Heer, *Rh. eridanii* Ung. and *Rh. aizoon* Ung.) occupy no clear systematic position; a re-examination of the fossil species belonging to this genus is needed (Jungwirth 2004, Kovar-Eder et al. 2004). Pollen grains attributed to *Rhamnus* have been found in several outcrops in the La Cerdanya Basin (Barrón 1996a: 276, pl. 21, figs 6–7). Finally, the alder buckthorn (*Frangula alnus* Mill.), the distribution of which covers most of temperate Europe (extending northward to central Britain and central Scandinavia) and western Asia (Meusel et al. 1978), also has leaves very similar to the studied specimen. However, alder buckthorn leaves show intersecondary veins, a feature not observed in the fossil specimen. Thus, it is not possible to assign the present specimens to the genus *Frangula*. In conclusion, the non-specific morphological features of the studied specimens, and the lack of cuticles, prevent their assignment to any particular genus of the family Rhamnaceae.

Rosaceae Juss. 1789

Rosaceae gen. et sp. indet.

Pl. 4, Fig. 7

1955 Dicotiledónea, sp. – Menéndez Amor, p. 182, pl. 51, fig. 4.

1992a *Fraxinus excelsior* L. (pars) – Barrón, p. 106, pl. 1, figs 7–8.

1996a *Fraxinus numana* Massalongo (pars) – Barrón, pp. 304–306, pl. 24, fig. 1.

Material: MGBV-9795; MNCNV-312, 924. These specimens were collected from unknown sites.

Description: Leaves elliptical-lanceolate, 5.1–5.7 cm long and 2.3–2.6 cm wide; apex acute; base cuneate, slightly asymmetrical in specimen MGBV-9795; margin serrate; teeth compound; teeth concave or straight on the apical side and convex or straight on the basal side; sinus acute and apex mucronate; petiole short 3.9–5 mm long. Midvein moderate and straight; venation pinnate semicraspedodromous; secondary venation curved with 5–6 pairs of secondary veins emerging at 40°; secondary vein spacing decreasing towards the base; weak intersecondaries; third order veins poorly preserved, partly percurrent and partly random reticulate; marginal ultimate venation not preserved.

Remarks: On the basis of venation, margin and leaf shape, the specimens might be assigned to *Prunus* or terminal leaflets of *Rosa*. Specimen MNCNV-924 shows margin features similar to those of *Prunus acuminata* Braun from Cantal (Roiron 1991: pl. 6, fig. 5), which has compound mucronate teeth. In addition, the shape and marginal teeth of specimen MNCNV-312 resemble those of *Rosa* sp. for the Pliocene of Willershausen (Knobloch 1998: pl. 36, fig. 3). However, the gross-morphology of the study specimen resembles leaflets of extant rosebush too, as well as the leaves of the extant *Prunus cerasus* L. of Europe and Southeast Asia. More specimens related to these fossils need to be studied for any confident generic assignment to be made.

Sapindaceae Juss. 1789

Acer L. 1753b

Acer pyrenaicum Rérolle emend.

Pl. 4, Fig. 8; Pl. 5, Figs 1–5

1884b *Acer trilobatum* Braun – Rérolle, p. 297, pl. 11, fig. 5.

1885 *Acer pyrenaicum* Rérolle – Rérolle, pp. 368–370, pl. 12, figs 2–6.

1885 *Acer magnini* Rérolle – Rérolle, pp. 370–371, pl. 13, figs 1–3.
1885 *Acer subrecognitum* Rérolle – Rérolle, pp. 371–372, pl. 13, figs 1–3.
1885 *Acer pseudocreticum* Ettingshausen – Rérolle, 4, pp. 373–374, pl. 14, figs 1.
1885 *Acer* sp. – Rérolle, pp. 372–373, pl. 13, fig. 5.
1945 *Acer magnini* Rérolle – Villalta & Crusafont, p. 345, pls 4, 10.
1945 *Acer pseudocraeticum* Ettingshausen – Villalta & Crusafont, p. 345, pl. 3.
1945 *Acer pyrenaicum* Rérolle – Villalta & Crusafont, Ilerda, 3, p. 345, pl. 4.
1945 *Acer trilobatum* Braun – Villalta & Crusafont, p. 345, pls. 5, 9.
1945 *Acer trilobatum* Braun var. *productum* Braun – Villalta & Crusafont, pp. 345, 350.
1947 *Acer pseudocreticum* Ettingshausen – Solé Sabarís & Llopis Lladó, p. 94, pl. 9.
1948 *Acer triangulilobum* Goeppert – Menéndez Amor, pp. 784–785, fig. 1c.
1955 *Acer magnini* Rérolle – Menéndez Amor, pp. 152–153, pl. 41, figs 2–3.
1955 *Acer pseudocreaticum* Ettingshausen – Menéndez Amor, p. 153, pl. 41, fig. 1.
1955 *Acer pyrenaicum* Rérolle – Menéndez pp. 154–156, pl.42, figs 1–2.
1955 *Acer subrecognitum* Rérolle – Menéndez Amor, p. 156.
1955 *Acer triangulilobum* Goeppert – Menéndez Amor, pp. 156–157.
1955 *Acer trilobatum* Braun – Menéndez Amor, pp. 157–159, pl. 40, fig. 1.
1955 *Sassafras ferretianum* Massalongo – Menéndez Amor, pp. 118–119, pl. 34, fig. 4.
1992b *Acer opalus* Miller – Barrón, pp. 546–548, pl. 1, figs 4–6, pl. 2, figs 1, 3–5.
1996a *Acer pyrenaicum* Rérolle – Barrón, pp. 283–289, text-fig. 59, pl. 22, figs 1–2.
1996b *Acer pyrenaicum* Rérolle – Barrón, pp. 44–48, pl. 1, figs 1–3, pl. 2, figs 1–4.
1996 *Acer pyrenaicum* Rérolle –Diéguez et al., pp. 337–338, pl. 3, figs 1–2.

Neotype: Specimen MGBV-9504 in the J. F. de Villalta collection, selected herein, held at the Natural History Museum of Barcelona (NAT) (Pl. 4, Fig. 7).

Occurrence: Coll de Saig outcrop (42° 22′ 2″N, 1° 49′ 20″W), in the ditches of local road 1411, which runs through a diatomite bed.

Other material examined: MGB-3980, 42716–42722, 42724–42729; MGBV-1715, 9480, 9498–9499, 9503, 9692, 9695, 9700, 9728, 9735, 9738, 9746, 9896, 10482, 10494, 10572, 10574, 11711–11712, 11715, 11717, 11734; MGM-1076M, 1078M, 1080M–1081M, 1097M, 1099M; MGSB-21771, 31198, 31225, 31315, 40414, 40444, 40451, 48126, 47027, 48127–48133, 48471; MNCNV-144, 329, 366, 368–373, 796, 799, 822, 3087, 3503–3504, 3525, 3527, 3533, 3542, 3553, 3566, 3588, 3591, 3608, 3614–3615, 3649, 4258, 4353, 4357, 4656–4657, 4659, 4663, 4665–4672, 4675, 4677, 4679–4681, 4683, 4685, 4687–4688, 4854, 4868–4870. These fossils were collected from all the mentioned outcrops of the La Cerdanya Basin (Text-fig. 1).

Original diagnosis: A. foliis crasse petiolatis, basi cordato-emarginatis, trilobatis vel rarius subquinquelobis, lobis subacutis, medio validiore, lateralibus sub angulo pleruumque acuto divergentibus, plus minus denticulatis vel crenulatis, nervis primariis secundariisque validis.

Emended diagnosis: Palmately tri- or pentalobed leaves elliptical to ovate; sinus between lobes at acute to right angles; apices acute; base rounded to slightly cordate; margin serrate except in the base which is entire; teeth acute and sometimes compound; petiole stout; venation basal actinodromous; lateral primary veins diverging at 30–55° from the midvein; when the leaf shows five lobes, the most basal primary veins emerge at 25–55° from the midvein; secondary venation craspedodromous or mixed craspedodromous; presence of intersecondary veins; tertiary venation percurrent; fourth order veins polygonal reticulate; freely ending ultimate veins absent or unbranched.

Description: Leaves elliptical to ovate, palmate, mainly trilobed (Pl. 5, Figs 1–2, 5), although pentalobed leaves also occur (Pl. 4, Fig. 8); size 2.9–7.9 cm long and 2–9.3 cm wide; some trilobed specimens show a medial lobe about twice the width of the lateral lobes (Pl. 5, Fig. 1); sinuses between lobes lie at acute and even right angles; pentalobed specimens show small lateral basal lobes 2–5 mm long (Pl. 4, Fig. 8); apices acute; base rounded to slightly cordate; margin serrate except at the base which is entire; teeth acute and sometimes compound with second and third order teeth (Pl. 5, Fig. 3); teeth straight to convex on the apical side and convex on the basal side; sinuses acute; tooth spacing usually irregular; petiole stout, 0.6–6.4 cm long and about 2 mm wide. Primary venation basal actinodromous (Pl. 4, Fig. 8; Pl. 5, Figs 1, 5); lateral primary veins diverging at 30–55° from the midvein; when the leaf has five lobes, the most basal primary veins emerge at 25–55° from the midvein; sometimes lateral primary veins dichotomise near the base; secondary venation craspedodromous or mixed craspedodromous; main and lateral primary veins bear 5–6 pairs of secondary veins that are straight or uniformly curved and arise from the midvein at 25–55°; secondary vein angle increases gradually towards

the base; secondary vein spacing decreases towards the base in the medial lobe but is uniform in the lateral lobes; sometimes several secondary veins dichotomise near their ends; intersecondary veins present; tertiary venation percurrent; fourth order veins polygonal reticulate; freely ending ultimate veins absent or unbranched (Pl. 5, Fig. 4); marginal ultimate venation looped.

Discussion: RÉROLLE (1885) described six different species of maples from leaf remains, either tri- or pentalobed with serrate margins. This author described four species for the first time: *Acer magnini* – characterised by lanceolate and trilobed specimens with longer and wider medial lobes than lateral lobes, *A. pyrenaicum* – distinguished by its tri- and pentalobed leaves with elliptical laminae, *Acer subrecognitum* – described from pentalobed and elliptical specimens as having scarce but patent marginal teeth, and *Acer* sp. – described from pentalobed specimens showing features similar to all of the aforementioned species. RÉROLLE (1884b, 1885) also identified the species *A. trilobatum* (STERNBERG) BRAUN (= *A. tricuspidatum* BRONN) from tri- and pentalobed specimens, and *A. pseudocreticum* ETTINGSHAUSEN from trilobed leaves similar to a specimen from the Messinian of Senigaglia (MASSALONGO & SCARABELLI 1859: pl. 15–16, fig. 9) which RÉROLLE also indicated similar to *A. pyrenaicum*. Within this group of six species, *A. pyrenaicum* has the most complete diagnosis and description, but it includes all the morphological characteristics of the other five species. The presence of *A. tricuspidatum* and *A. pseudocreticum* has not been corroborated for the La Cerdanya Basin; all the specimens studied can be assigned to *A. pyrenaicum*.

The taxonomic affinities between *A. pyrenaicum* and other maples remain unclear. WALTHER (1972) was the first to include *A. pyrenaicum* within *A. tricuspidatum* (as *A. tricuspidatum* BRONN subsp. *lusaticum* WALTHER). Later, STRÖBITZER-HERMANN (2002) changed the status of *A. tricuspidatum* subsp. *lusaticum*, reducing it to *A. tricuspidatum* form *pyrenaicum* (RÉROLLE) STRÖBITZER-HERMANN. According to STRÖBITZER-HERMANN & KOVAR-EDER (2002), *A. pyrenaicum* may be considered an evolutionarily young leaf-form of *A. tricuspidatum* on the basis of leaf morphological characteristics and some abaxial cuticle features. Thus, leaves assigned to *A. pyrenaicum* may in fact be leaves of *A. tricuspidatum* showing adaptations to edaphic and climatic conditions (including sun-exposure), which explains the co-occurrence of both species at several sites. However, the results of cuticular studies of Greek specimens of *A. pyrenaicum* do not relate this species to *A. tricuspidatum* or any other species of the section *Rubra* PAX (KVAČEK et al. 2002).

Another means of identifying the relatives of *A. pyrenaicum* involves studying the higher range venation of the fossil leaves. This led to the existence of two groups in the genus *Acer* (TANAI 1978). The present specimens can be related to the second group, whose members mostly have single, freely-ending veinlets (though they may be lacking); very rarely these may ramify once within the areoles. In fact, the areoles of the present specimens closely resemble those of the section *Acer,* in which fine veinlets are mostly lacking or rarely single within quadrangular areoles. They also resemble those of the maples of the section *Goniocarpa* POJARKOVA. Within this section, *A. opalus* MILL., *A. obtusatum* WALDST. and *A. hyrcanum* FISCH show features most similar to those of the present specimens. In addition, in the section *Rubra* (which includes *A. tricuspidatum*), the freely-ending veinlets are mostly single (rarely lacking) within quadrangular or pentagonal areoles; rarely they may also ramify just once.

Specimens similar to *A. pyrenaicum* have been described as *Acer* cf. *ilnicense* IL'INSKAJA from the late Miocene from Bavaria (KNOBLOCH 1988), *Acer nicolai* BOULAY from the Pliocene of Théziers (BOULAY 1890), and *Acer opulifolium* VILL. from the Pleistocene of the Scandorge Massif (LEROY & ROIRON 1996). A future review might relate these specimens to *A. pyrenaicum*. *A. pyrenaicum* was frequent in the Neogene floras of southern and southwestern Europe, which were sclerophyllous in nature (WALTHER & ZASTANIAK 2005). Frequently, *A. pyrenaicum* was parasitised by acari of the genera *Artacris* and *Eriophyes* (DIÉGUEZ et al. 1996).

Ulmaceae MIRBEL 1815

Ulmus L. 1753a

Ulmus cf. *plurinervia* UNGER 1843

Pl. 5, Fig. 6

1843 *Ulmus plurinervia* UNGER, pp. 95–96, pl. 25, figs 1–4.

1996a *Ulmus* sp. – BARRÓN, pp. 128–131, text-fig. 26, pl. 10, fig. 5.

Material: MGBV-10484; MGSB-31311, 481150; MNCNV-711, 4513, 4530. These specimens were collected from the Coll de Saig, Beders and Balltarga outcrops.

Description: Leaves elliptical to ovate or slightly obovate with lamina 1.6–3.75 cm long and 0.7–2.1 cm wide; apex acute; base convex to rounded, sometimes asymmetrical; margin serrate with compound teeth; secondary order teeth present; petiole 0.1–1.1 cm long. Midvein stout and straight; venation pinnate craspedodromous; secondary venation straight and uniformly spaced with 10–12 pairs of secondary veins arising at 45–65°; several secondary veins dichotomise close to the teeth; tertiary venation percurrent; fourth order veins polygonal reticulate; marginal ultimate venation looped.

Remarks: *Ulmus* is an anisophyllous and heterophyllous genus. Indeed, a significant number of species have been described from leaves with different morphologies. This is the case of *Ulmus longifolia*, *Ulmus carpinoides* and *Ulmus pyramidalis*, which were described by GOEPPERT (1855). These should really be considered forms of *U. carpinoides* (VON SCHLECHTENDAL 1896, KOVAR-EDER 1988).

The few specimens collected from the La Cerdanya Basin outcrops do not differ from the leaves of *U. plurinervia* of the Sarmatian of Erdőbénye, Hungary (KOVÁTS 1856: pl. 4, figs 8–12). Similarly, they coincide with the specimen of *Ulmus* sp. from the early Miocene of Kreuzau (Germany) (FERGUSON 1971: fig. 19J, pl. 13, fig. B). Unfortunately, the appearance of the studied specimens does not exactly coincide with the types reported by UNGER (1843); fossils of the latter show more ovate and symmetrical laminae with shorter petioles and a larger number of secondary veins. The La Cerdanya Basin specimens are therefore attributed (with some doubts) to *U. plurinervia*. On the basis of leaf morphology, *U. plurinervia* might be regarded as related to the extant East Asian representatives *U. pumila* L. and *U. parvifolia* JACQ. (ZASTAWNIAK 1980). The genus *Ulmus* was previously identified in the basin from rounded samari with irregular, reticulate venation (MENÉNDEZ AMOR 1955: pl. 30, fig, 5, BARRÓN 1996a: text-fig. 27, pl. 10, fig. 1). The latter author attributed these fruits to *Ulmus braunii* HEER.

Dicotyledonae inc. sed.

Dicotylophyllum BANDUSKA 1923 (non SAPORTA 1892)

Dicotylophyllum sp.

Pl. 5, Fig. 7

1945 *Sapindus endulatis* BRAUN – VILLALTA & CRUSAFONT, pl. 9.

Material: MGBV-9497. This specimen was collected from the Coll de Saig outcrop.

Description: Possible leaflet lanceolate, asymmetrical, 5.5 cm long and 1.51 cm wide; apex rounded; base slightly asymmetrical; margin serrate, undulate in the basal part on its left side; sinuses rounded; teeth acuminate; petiolule 1 mm long. Midrib straight and stout; secondary venation cladodromous; secondaries curved, irregularly spaced, with 10 pairs of secondary veins arising at different angles from the midvein at 45–80°; some veins from the left side of the leaf dichotomising at about one-third of the distance to the margin; vein angle wider in the basal area of the right side and near the apex; secondaries looped near the margin; intersecondary veins present; tertiary venation percurrent; marginal ultimate venation not preserved.

Remarks: This specimen has been compared with the genera *Sapindus* and *Zelkova* (VILLALTA & CRUSAFONT 1945, BARRÓN 1996a). However, its asymmetrical shape and the presence of dichotomies in the secondary veins preclude its association with them. It might be compared with leaflets of certain genera of the family Anacardiaceae, such as *Pistacia* L., *Rhus* L. or *Cotynus* MILL., given the cladodromous venation shown by several member species as well as the dichotomies of the secondaries. Nonetheless, given the lack of more similar specimens with which to make comparisons, and the lack of any cuticular remains, the systematic affinity of the studied specimen remains unclear.

Smilacaceae VENTENANT 1799

Smilax L. 1753b

Smilax cf. *aspera* L. 1753b var. *fossilis*

Pl. 5, Fig. 9

1945 *Smilax* cf. *obtusangula* HEER – VILLALTA & CRUSAFONT, pp. 344, 347.

1996a *Smilax hastata* (BROGNIART) SAPORTA – BARRÓN, pp. 330–332, text-fig. 67, pl. 28, fig. 3.

Material: CMLL-053. This specimen was collected from the Torrent de Vilella outcrop.

Description: Leaf almost complete, lanceolate, 3.1 cm long and 1.6 cm wide; apex missing; base hastate; margin entire; petiole absent. Midrib straight and moderate; venation suprabasal acrodromous; two pairs of thin, lateral primary veins; secondary veins arising perpendicularly to the primary veins; third

order venation and marginal ultimate venation not preserved.

Remarks: The studied specimen is fragmentary and shows morphological features similar to those of several fossil species. It resembles *Smilax obtusifolia* HEER in terms of its hastate base, although the latter species has three pairs of lateral primary veins (HEER 1855: pl. 30, fig. 9). A similar species, *Smilax haidingeri* UNGER, sometimes shows a hastate base and the same number of veins (ETTINGHAUSEN 1851, pl. 2, fig 33). *Smilax sagittifera* HEER has lanceolate laminae with sagittate bases and a larger number of primary veins (HEER 1855: pl. 30, fig. 7, HEER 1859: pl. 157, fig. 21, KOVAR-EDER et al. 2004: pl. 11, fig. 19). The studied specimen has been related to *Smilax hastata* (BRONGNIART) SAPORTA by comparison with two fragmentary specimens from the early–middle Miocene of Moravia (KNOBLOCH 1969: text-figs. 63–64), although they do not preserve the secondary and tertiary venation. The most similar fossil specimen comes from the Pliocene of Turkey, which was identified as *Smilax aspera* L. *fossilis* (KASAPLIGIL 1977: fig. 17). Its shape, base and venation closely resemble those of the studied specimen. Similar leaves are seen in the extant *S. aspera* L., which is widespread in the Mediterranean region, and in *Smilax pendulina* LOWE, which occurs in Macaronesia.

5 Discussion and comparisons

The macroflora of the La Cerdanya Basin involves 31 plant families and 71 species (see Table 1). It is therefore one of the most diverse late Miocene plant assemblages known for southwestern Europe. Pteridophytes are represented by three genera – *Equisetum*, *Pteridium* and *Osmunda* – which now are currently distributed worldwide (RÉROLLE 1884a, MENÉNDEZ AMOR 1955, BARRÓN 1996a). Ginkgophytes are represented by the common Neogene species *Ginkgo adiantoides* (UNGER) HEER, a relative of the East Asian *G. biloba* L. (HABLY & FERNÁNDEZ MARRÓN 2007). Conifers are represented by nine taxa whose relatives now mainly inhabit North America and East Asia. Angiosperms are the most diverse group with 44 genera and 58 species, with relatives in Eurasia and North America. At the family level, Betulaceae, Fagaceae, Lauraceae and Sapindaceae are the best represented. The presence of the 27 dicotyledonous taxa mentioned by VILLALTA & CRUSAFONT (1945) and MENÉNDEZ AMOR (1955) requires confirmation since they were described from poorly preserved fossils (see Table 2).

Given the composition of the Palaeogene floras of the boreal regions (MEYEN 1987), the La Cerdanya Basin assemblages can be said to include 40 taxa of the modern Arctotertiary type which means broadleaved deciduous plants (57.14%). Nineteen taxa (27.14%) belong to the Palaeotropical (broadleaved evergreen) type, the Lauraceae being the best represented. KOVAR-EDER et al. (2006) calculated the percentage of broadleaved deciduous (59.8%) and broadleaved evergreen vegetation (27.8%) for the late Miocene and Pliocene of southern Europe using IPR vegetation analysis data (KOVAR-EDER et al. 2008, TEODORIDIS et al. 2011). These data are, respectively, almost coincident with percentage composition (Arctotertiary and Palaeotropical taxa) of the late Miocene megaflora of the La Cerdanya Basin.

Many well known late Miocene plant sites have been recorded in the Mediterranean Tethys bioprovince (sensu MAI 1995), but few have been described from the Iberian Peninsula. Further, a number of these Iberian sites are characterised by assemblages of very low diversity, e.g., at the Libros outcrop and at sites in the Lisbon area (MELÉNDEZ MELÉNDEZ 1945, FERNÁNDEZ MARRÓN 1972, TEIXEIRA & PAIS 1976, PAIS 1986). Although in need of profound palaeobotanical revision, the macroflora of Catalonia's La Seu d'Urgell Basin (which is similar in age) shares many similarities with the flora of the La Cerdanya Basin (SANZ DE SIRIA 1980b, SANZ DE SIRIA 1994). The La Bastida site in the La Seu d'Urgell Basin is characterised by the presence of *Alnus occidentalis* and different species of *Acer*, *Alnus*, *Fagus*, and *Populus*. The Acueducto outcrop, in contrast, is characterised by evergreen and deciduous taxa belonging to Fabaceae, Lauraceae, Moraceae and Sapindaceae, and the species *Alnus occidentalis*, *Quercus hispanica*, *Ulmus braunii* HEER and *Zelkova zelkovifolia* (UNGER) BŮŽEK & KOTLABA.

Furthermore, the flora of the early Vallesian of La Bisbal (Baix Empordá; Catalonia) shows the great abundance of deciduous elements (75% of the studied remains), with species belonging to *Acer*, *Alnus*, *Pterocarya*, *Platanus*, *Ulmus* and *Zelkova*. The remainding elements (25%) are evergreen taxa mainly represented by *Daphnogene polymorpha* (BRAUN) ETTINGSHAUSEN (SANZ DE SIRIA 1993). Similarly, some 49% of the late Vallesian macroflora of Terrassa (Vallès Occidental) consists of deciduous elements such as *Acer*, *Alnus*,

Carya, *Fraxinus*, *Quercus*, *Tilia* and *Zelkova*. Evergreen taxa (51%) are oaks and other warm-temperate to subtropical dicotyledonous genera (e.g., *Sapindus*, *Myrsine*, Lauraceae) (SANZ DE SIRIA 1997).

The flora from the La Cerdanya Basin may be included in the "Broadleaved Deciduous Forests with some evergreens and coniferous taxa" for the Miocene of western Eurasia (UTESCHER et al. 2007). Although broadleaved deciduous trees clearly dominated the assemblages (e.g., *Acer*, *Carpinus*, *Quercus* and *Fagus*), evergreen trees also occurred (e.g., *Laurophyllum* sp.), and the conifers reached a comparatively high diversity including nine taxa: *Pinus palaeostrobus*, *Pinus* sp., *Torreya bilinica*, *Cryptomeria anglica*, *Abies saportana*, cf. *Tsuga* sp. and Cupressaceae gen. et sp. indet. (2 species) and Pinaceae gen. et sp. indet. (Table 1). According to MAI (1995), the occurrence of the conifers *A. saportana*, cf. *Tsuga* sp. and *Pinus* spp. in the La Cerdanya Basin, as well as the appearance of a significant group of species belonging to the genera *Acer*, *Alnus*, *Betula*, *Carpinus*, *Laurophyllum*, *Ostrya*, *Quercus* and *Tilia* relate this flora with the Likudi-Vegora complex ("Florenkomplex"), which depeloped in the Mediterranean Tethys phytoprovince over the late Miocene.

The late Miocene macrofloras of northern Greece have also taxa in common with that of the La Cerdanya Basin. Species such as *Osmunda parschlugiana*, *Ginkgo adiantoides*, *Acer integerrimum*, *A. pyrenaicum*, *Betula pseudoluminifera*, *Carpinus grandis*, *Fagus gussonii*, *Hedera multinervis*, *Laurophyllum pseudoprinceps*, *Pterocarya paradisiaca*, *Quercus drymeja*, *Q. mediterranea*, and *Zelkova zelkovifolia* have been identified at different sites (KNOBLOCH & VELITZELOS 1986, KNOBLOCH & VELITZELOS 1987, VELITZELOS & KVAČEK 1999, KVAČEK et al. 2002, VELITZELOS et al. 2014). Most of the identified species were widely distributed across central Europe during the Neogene. *Glyptostrobus europaeus* (BRONGNIART) UNGER, *Fagus gussonii*, *Quercus drymeja* and *Q. sosnowskyi* are well represented in the flora of Vegora (KVAČEK et al. 2002), *F. gussonii* and *Quercus* cf. *drymeja* are abundant in that of Likoudi (KNOBLOCH & VELITZELOS 1986, KNOBLOCH & VELITZELOS 1987), and *Quercus* cf. *mediterranea* is common in that of Prosilio (KNOBLOCH & VELITZELOS 1986, KVAČEK et al. 2002). The assemblages at Drymos, in contrast, are numerically dominated by conifers (KVAČEK et al. 2002).

It is possible to carry out a general comparison between the macroflora from La Cerdaña Basin and that from Vegora using previous climatic studies. So, the climatic proxies obtained using the Coexistence Approach method for Vegora are: mean annual temperature (MAT) 13.3–14.6 °C, mean temperature of the coldest month (CMT) 0.4–4.5 °C, mean temperature of the warmest month (WMT) 23.8–24.6 °C and mean annual precipitation (MAP) 897–1018 mm (KVAČEK et al. 2002). These values are only slightly lower than those obtained from a preliminary work for the La Cerdanya Basin (BARRÓN et al. 2010) employing the list of taxa provided by BARRÓN (1996a), which are: MAT 14.4–15.8 °C, CMT 3.7–5.2 °C, WMT 25.7–26.4 °C and MAP 1231–1355 mm. These similar results show a clear resemblance between the La Cerdanya and Vegora macrofloras from a palaeoclimatic point of view, supporting the connection between the macroflora of the La Cerdanya Basin and the Likudi-Vegora complex. The flora from the La Cerdanya Basin also resembles those of the late Miocene of Italy. The most representative Italian macrofloras are those of the Messinian age (MASSALONGO & SCARABELLI 1859, BALDUZZI et al. 1980, BERTINI & MARTINETTO 2011). These are rich and diverse, and characterised by temperate to warm-temperate elements such as *Pinus*, *Pseudotsuga*, *Sciadopitys*, *Acer*, *Alnus*, *Betula*, *Carpinus*, *Carya*, *Celtis*, *Fagus*, *Quercus*, *Liquidambar*, *Magnolia*, *"Parrotia"*, *Populus*, *Pterocarya*, *Salix*, *Tilia*, *Ulmus*, and *Zelkova*, and scarce thermophilous taxa such as Araliaceae, *Buxus*, *Engelhardia*, Lauraceae, *Myrica*, *Platanus*, *Trigonobalanopsis*, and *Smilax*.

Some analogies might also be drawn with Miocene floras from localities situated in the Atlantic-Boreal phytoprovince (sensu MAI 1995). Thus, the composition of the late Miocene macrofloras of the Massif Central, Haute-Loire, Ardèche and Cantal (France) (BOULAY 1887, MARTY 1903, MARTY & GLANGEAUD 1936, GRANGEON 1953, GRANGEON 1958, CHARRE & GRANGEON 1967, ROIRON 1991, ROIRON 1992) resemble those of the La Cerdanya Basin. The former floras are composed mainly of deciduous woody plants belonging to the genera *Fagus*, *Populus*, *Betula*, *Carpinus*, *"Parrotia"*, *Populus*, *Salix*, *Zelkova*, *Acer*, etc. However, *Quercus hispanica* is also very common. In addition, these floras include taxa not found in the La Cerdanya Basin, such as *Sequoia*, *Picea*, *Engelhardia*, *Liquidambar*, *Celtis*, and *Juglans*. Evergreen taxa are scarce in these floras. The most

conspicuous taxa are Lauraceae, *Quercus drymeja* UNGER and *Q. mediterranea* UNGER, along with species belonging to the genera *Berchemia*, *Myrica*, *Hedera*, *Buxus*, *Dombeyopsis* and *Ilex*. In contrast, the Messinian flora of Murviel-les-Beziers (AMBERT & ROIRON 1990) is composed of a mixture of broadleaved deciduous trees (*Populus*, *Liquidambar*, *Acer* and *Platanus*) and genera with subtropical affinities such as *Cedrela* and *Zanthoxylum*.Although the late Miocene and Pliocene floras of northern and central Europe share taxa with the La Cerdanya Basin, deciduous taxa are usually predominant at these sites. Such is the case of the upper Pannonian–Pontian flora of Aubenham (Bavaria), which has no evergreen elements (KNOBLOCH 1988), or the Vallesian flora of Sprendlingen (Germany), which is dominated by the taxodioid conifers, *Acer* and Betulaceae and deciduous *Quercus*, *Salix*, *Ulmus* and *Zelkova*, but very few evergreen elements belonging to the families Lauraceae and Fabaceae (MELLER 1989). Also in Germany, in the Ottendorf-Okrilla flora can be found a deciduous riparian forest with only occasional occurrence of some thermophilous species such as *Taxodium dubium* (STERNBERG) HEER emend KUNZMANN, KVAČEK, MAI & WALTHER, *Liquidambar europaea* BRAUN, "*Parrotia*" *pristina* or *Cercidiphyllum crenatum* (UNGER) R.W. BROWN (WALTHER & EICHLER 2010). Floras of similar composition are reported for other late Miocene and Pliocene sites such as those of Sośnica, Bełchatów, and Ruszów in Poland (ŁAŃCUCKA-ŚRODONIOWA et al. 1981, HUMMEL 1983, WOROBIEC & LESIAK 1998), Chiuzbaia in Romania (GIVULESCU 1990), Moravia (KNOBLOCH 1969), Molassezone of Austria (KOVAR-EDER 1988), Hungary (HABLY 2003), and Limburg in The Netherlands (LAURENT & MARTY 1923). KNOBLOCH (1992) compared the flora of the La Cerdanya Basin with that of the Pliocene of Willershausen. However, the latter, less ancient flora, is very diverse and rich in deciduous and mesophilous taxa that are absent in the La Cerdanya Basin (e.g., *Aesculus*, *Actinidia*, *Cercidiphyllum*, *Liquidambar*, *Liriodendron*, roburoid *Quercus*, *Sorbus* and *Swida*), and its evergreen taxa are represented by *Comptonia*, *Buxus*, *Dombeyopsis*, *Hedera*, *Leguminosites*, *Sassafras* and *Cedrela* (KNOBLOCH 1998).

6 Summary

The present study describes new plant records from the late Miocene macroflora of the La Cerdanya Basin in Spain, and complements the descriptions of selected species established by RÉROLLE at the end of the 19th century. This flora includes vascular cryptogams, conifers, woody broadleaved deciduous and broadleaved evergreen dicotyledons, herbaceous dicotyledons, and monocotyledons plants linked to damp places. From leaf remains and diaspores, RÉROLLE described 12 species and three varieties of plants for the basin: *Abies saportana*, *Acer magnini*, *Acer pseudocreticum*, *Acer pyrenaicum*, *Acer subrecognitum*, *Alnus occidentalis*, *Parrotia gracilis*, *Potamogeton orbiculare*, *Quercus hispanica*, *Tilia vidali*, *Trapa ceretana*, *Zelkova subkeaki*, *Buxus sempervirens* var. *ceretana*, *Fagus pliocenica* var. *ceretana* and *Populus canescens* (*pliocenica*). On the basis of newly studied morphological features of seed and leaf specimens, the present study provides the synonyms of most of these and gives emendations to the deiagnoses of *Abies saportana*, *Acer pyrenaicum*, *Alnus occidentalis*, *Quercus hispanica* and *Tilia vidali*.

The present work suggests that the La Cerdanya macroflora is composed of 30 families including 43 genera and 71 species. The first horsetail for this flora is described, as well as three new conifers, 19 arboreal or bushy dicotyledonous angiosperms, and one monocotyledonous angiosperm. The taxa identified are mainly of the broadleaved deciduous modern Arctotertiary type (57.14%); Broadleaved evergreen (Palaeotropical) elements and other elements are less well represented though still quite common (27.14% and 15.72%, respectively). The families Betulaceae, Fagaceae, Lauraceae and Sapindaceae are the most frequent representatives in the taphocoenoses. Some 27 taxa previously cited need to be confirmed via the study of new, better preserved specimens (Table 2). The diversified macrofloral assemblage recorded does not differ greatly from those of other western European sites of similar age. The nearby and coeval macroflora of the Seu d'Urgell Basin shows strong similarities. In terms of floristic composition, the Greek late Miocene floras have similar composition to that of La Cerdanya relating it to the Likudi-Vegora complex ("Florenkomplex") of the Mediterranean Tethys phytoprovince. Likewise, French late Miocene sites of the Massif Central, Haute-Loire, Ardèche and Cantal also have floras similar to that of the La Cerdanya Basin.

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5 plates and explanation of plates

Plate 1

Fig. 1. *Equisetum* sp. Detail of the specimen MNCNV-4830 from the Carrer de Pi outcrop.
Fig. 2. Cupressaceae gen. et sp. indet. Specimen MGBV-47049 from an unknown site in the La Cerdanya Basin. Shoot with two imbricated facial scale-like leaves.
Fig. 3. *Abies saportana* RÉROLLE emend. Specimen MNCNV-4769 from the Barranc de Salanca outcrop. Obovate seed with near triangular wing. The seed is held in a deep cup (a).
Fig. 4. *Abies saportana* RÉROLLE emend. Specimen MGM-318M (neotype) from the Coll de Saig outcrop. Obovate seed with near-triangular wing.
Fig. 5. *Abies saportana* RÉROLLE emend. Specimen MNCNV-3093 from the Beders outcrop.
Fig. 6. *Tsuga* sp. Specimen MGSB-69390 from the Pedra outcrop. Elliptical, symmetrical cone compression showing broadly ovate to orbicular seed scales.
Fig. 7. *Tsuga* sp. Specimen MGM-48M from the Coll de Saig outcrop. Cone impression.
Fig. 8. Pinaceae gen. et sp. indet. Specimen MNCV-4743 from the Barranc de Salanca outcrop. Wide obovate seed scale with entire margin and convex apex, which seems to be attached to a bract scale-like structure (a).

Scale bar represents 5 mm.

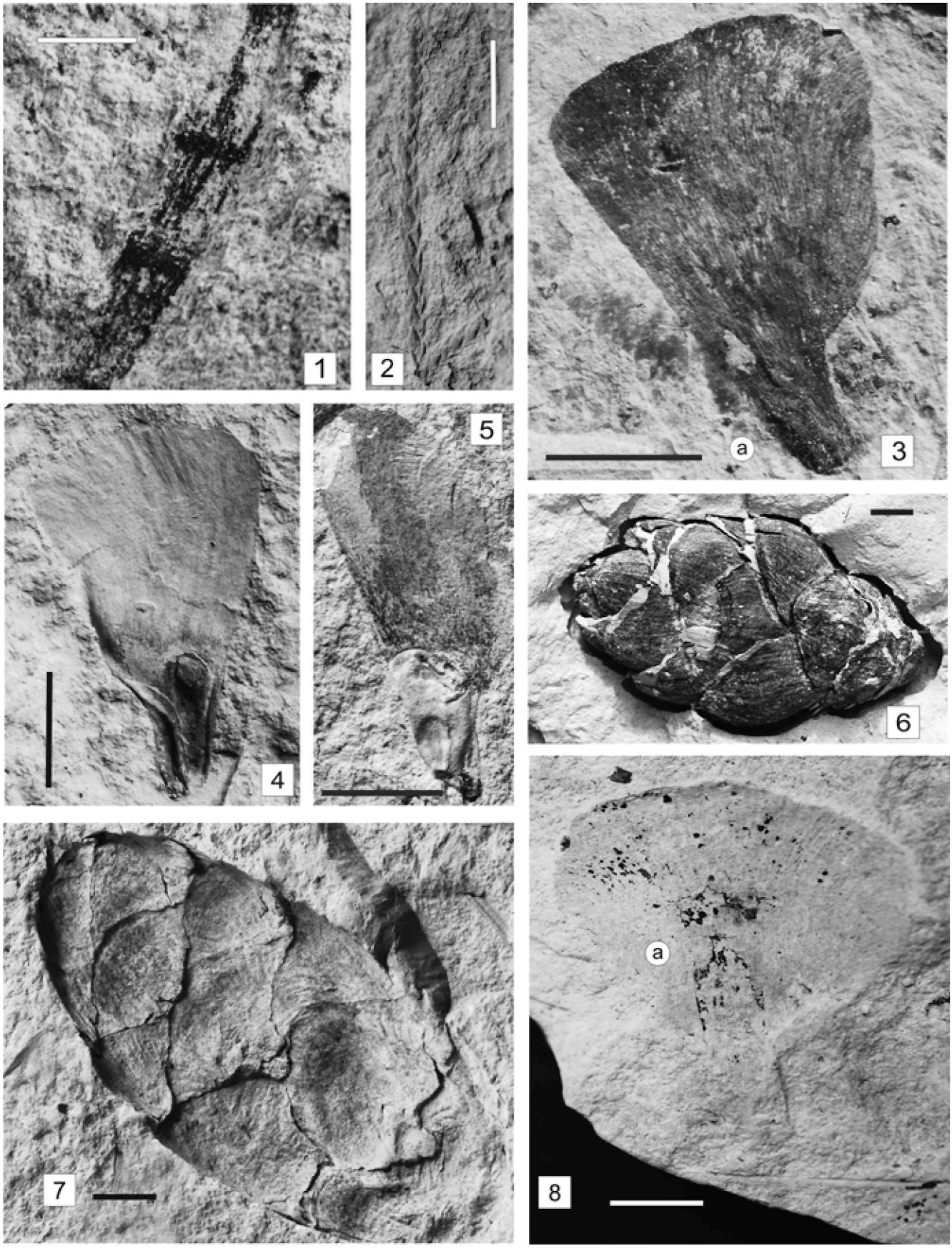
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Plate 2

Fig.1. *Hedera* cf. *multinervis* Kolakovskii. Specimen MGSB-69146 from the Pedra outcrop. Elliptical asymmetrical leaf with entire, irregularly undulate margin.

Fig. 2 *Mahonia* cf. *pseudosimplex* Kvaček & Walther. This specimen (MGBV-9712) from the Prats outcrop shows spiny, large teeth (a) on coarsely simple serrate margin.

Fig. 3. *Alnus occidentalis* Rérolle emend. Specimen MGBV-9492 (neotype) from the Coll de Saig outcrop. Elliptical leaf with acuminate apex.

Fig. 4. *Alnus occidentalis* Rérolle emend. Specimen MNCNV-4371 from the Torrent de Vilella outcrop. Orbicular leaf showing acute, sharply pointed teeth and irregular tooth spacing (a) located in the upper two thirds of the lamina.

Fig. 5. *Alnus occidentalis* Rérolle emend. Specimen MNCNV-4371. Detail of the retuse apex.

Fig. 6. *Alnus* sp. Specimen MGB-44060 from the Coll de Saig outcrop. General view of the specimen showing pinnate craspedodromous venation.

Fig. 7. *Alnus* sp. Specimen MGB-44060. Detail of the apex and compound teeth.

Fig. 8. *Caesalpinites* sp. Specimen MNCNV-352 from the Barranc de Salanca outcrop. Elliptical leaflet with rounded apex and base and entire margin.

Fig. 9. *Caesalpinites* sp. Specimen MNCNV-337 from the Prats outcrop.

Scale bar 1 cm.


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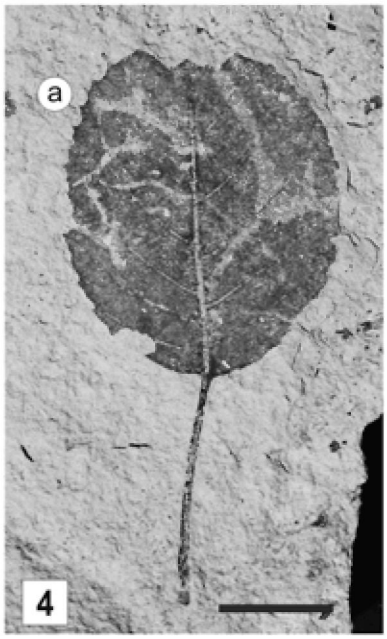
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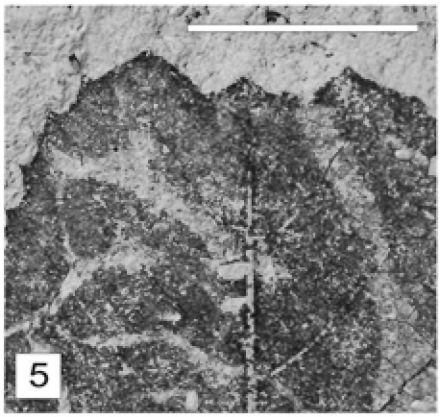
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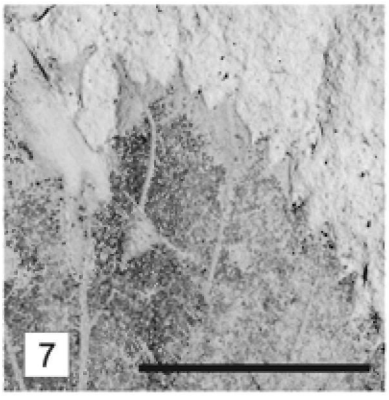
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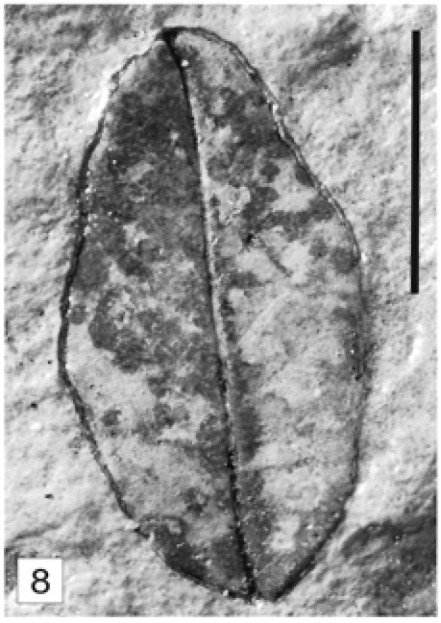
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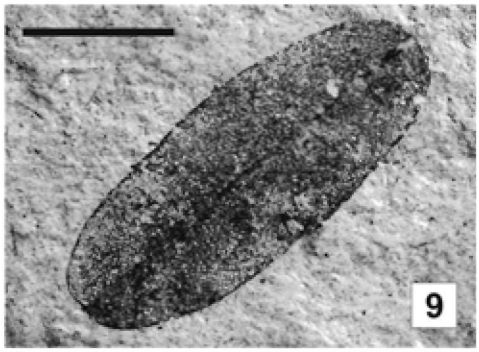
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Plate 3

Fig. 1. *Leguminocarpon* sp. 1. Specimen CJQ-013 from the Coll de Saig outcrop. Unilocular pod with seed chamber externally visible.

Fig. 2. *Leguminocarpon* sp. 2. This specimen (CJQ-014) from the Coll de Saig outcrop shows one series of 10 orbicular to rounded seeds inserted along the axis of the pod.

Fig. 3. Fabaceae gen. et sp. indet. Specimen MNCNV-334 from the Coll de Saig outcrop. Ovate leaflet with retuse apex.

Fig. 4. *Quercus hispanica* Rérolle emend. Specimen MGM-1063M (neotype) from the Pedra outcrop. Leaf mainly obovate showing the simple serrate margin in the upper two thirds of the lamina (a).

Fig. 5. *Quercus hispanica* Rérolle emend. Specimen MNCNV-4286 from the Coll de Saig outcrop showing pinnate mixed craspedodromous venation (b).

Fig. 6. *Quercus* sp. Specimen MGBV-9493 from the Coll de Saig outcrop. Elliptical leaf with simple serrate margin and small teeth.

Fig. 7. *Laurophyllum* sp. Specimen MGBV-9490 from the Coll de Saig outcrop. Elliptical leaf with straight petiole.

Fig. 8. cf. *Laurophyllum* sp. Specimen MGB-42782 from the Coll de Saig outcrop. Obovate leaf with acuminate apex and pinnate weak brochidodromous venation.

Fig. 9. *Tilia vidali* Rérolle emend. Detail of the specimen MNCNV-288 (neotype) from the Coll de Saig outcrop showing actinodromous basal venation with 3–5 primary veins (a) and percurrent tertiary venation (b).

Fig. 10. *Tilia vidali* Rérolle emend. Detail of the specimen MNCNV-4707 from the Barranc de Salanca outcrop showing a compound serrate margin and agrophic veins.

Scale bar 1 cm.

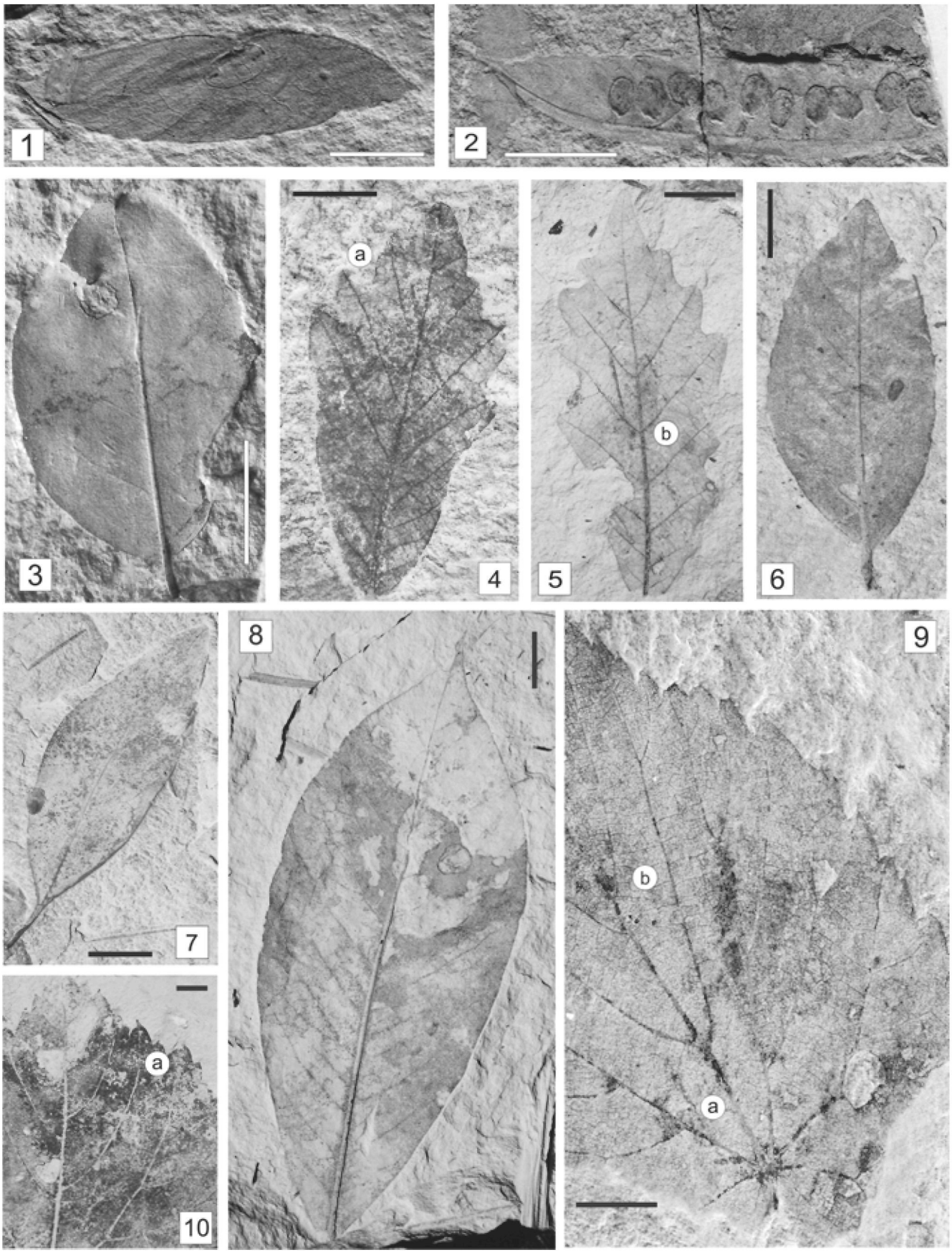
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Plate 4

Fig. 1. *Tilia vidali* Rérolle emend. Specimen MNCNV-4706 from the Barranc de Salanca outcrop. SEM photo of a poorly preserved cuticle showing (a) elongated rectangular epidermal ordinary cells on the tertiary veins (b) poorly preserved epidermal isodiametric cells on an areole and (c) anomocytic stomata.

Fig. 2. *Tilia vidali* Rérolle emend. Specimen MNCNV-4706. SEM photo of vessels with circular pit-like structures (a).

Fig. 3. *Tilia vidali* Rérolle emend. Specimen MNCNV-4704 from the Barranc de Salanca outcrop. Oblong leaf-like bract.

Fig. 4. *Cedrela heliconia* (Unger) Knobloch. Specimen BC-1115 from the Coll de Saig outcrop. Lanceolate leaflet.

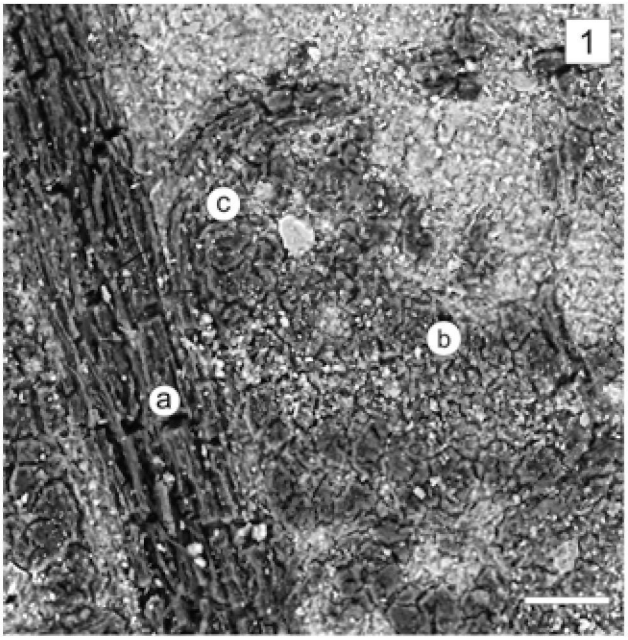
Fig. 5. cf. *Myrica* sp. Specimen MNCNV-4558 from the Balltarga outcrop. Narrow elliptical leaf with pinnate craspedodromous venation.

Fig. 6. Rhamnaceae gen. et. sp. indet. Specimen MNCNV-4701 from the Coll de Saig outcrop. Elliptical leaf with pinnate eucamptodromous venation and percurrent tertiary veins.

Fig. 7. Rosaceae gen. et sp. indet. Specimen MNCNV-924 from an unknown site in the La Cerdanya Basin. Elliptical leaf with acute apex and serrate margin.

Fig. 8. *Acer pyrenaicum* Rérolle emend. Specimen MGBV-9504 (neotype) from the Coll de Saig outcrop. General view of a pentalobed leaf.

Scale bar 1 cm except Fig. 1: 100 μm and Fig. 2: 50 μm.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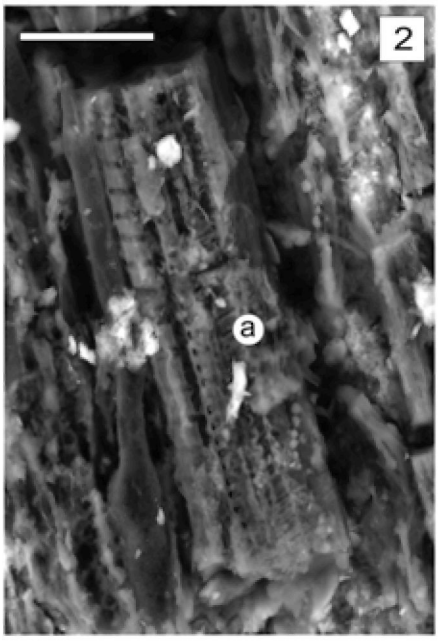
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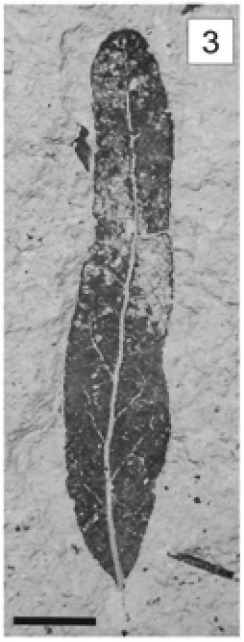
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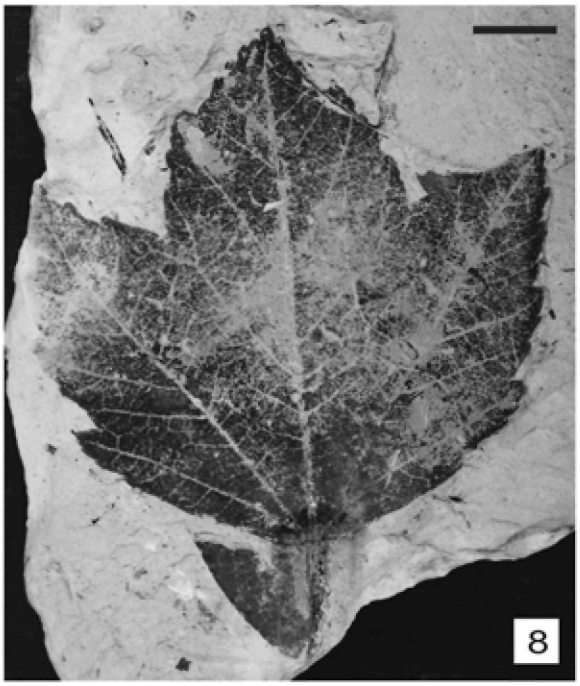
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Plate 5

Fig. 1. *Acer pyrenaicum* RÉROLLE emend. Specimen MGBV-9481, palmately trilobed leaf with medial lobe about twice the width of the lateral lobes.

Fig. 2. *Acer pyrenaicum* RÉROLLE emend. Detail of the palmately trilobed specimen MGM-1076M from the Coll de Saig outcrop. General appearance of the leaf margin and venation.

Fig. 3. *Acer pyrenaicum* RÉROLLE emend. Specimen MGM-1076M. Appearance of the secondary pinnate craspedodromous venation (a), percurrent tertiary venation (b) and irregular tooth spacing (c).

Fig. 4. *Acer pyrenaicum* RÉROLLE emend. Specimen MGM-1076M. Stereomicroscope image of polygonal reticulate free-ending fourth order veins; ultimate veins absent or unbranched (a).

Fig. 5. *Acer pyrenaicum* RÉROLLE emend. Specimen MGBV-9503 from the Coll de Saig outcrop. General view of palmately trilobed specimen with stout petiole.

Fig. 6. *Ulmus*.cf. *plurinervia* UNGER. Specimen MNCNV-4513 from the Coll de Saig outcrop. Elliptical leaf with pinnate craspedodromous venation.

Fig. 7. *Dicotylophyllum* sp. Specimen MGBV-9497 from the Coll de Saig outcrop. Asymmetrical lanceolate leaflet.

Fig. 8. *Decodon* sp. Specimen MGBV-9523 from the Coll de Saig outcrop. Lanceolate leaf.

Fig. 9. *Smilax* cf. *aspera* L. var. *fossilis*. Specimen CMLL-053 from the Torrent de Vilella outcrop. Fragmentary lanceolate leaf with hastate base.

Scale bar 1 cm, except Fig. 4, in which it represents 2 mm.


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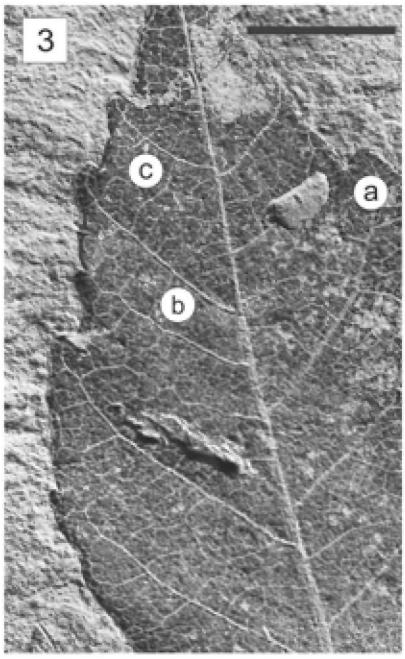
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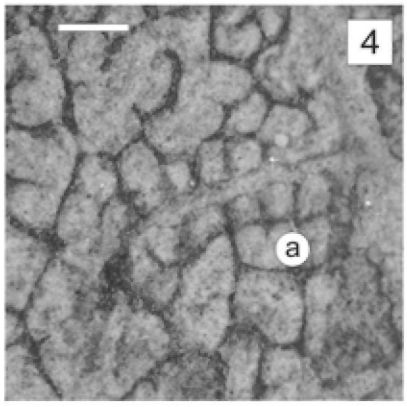
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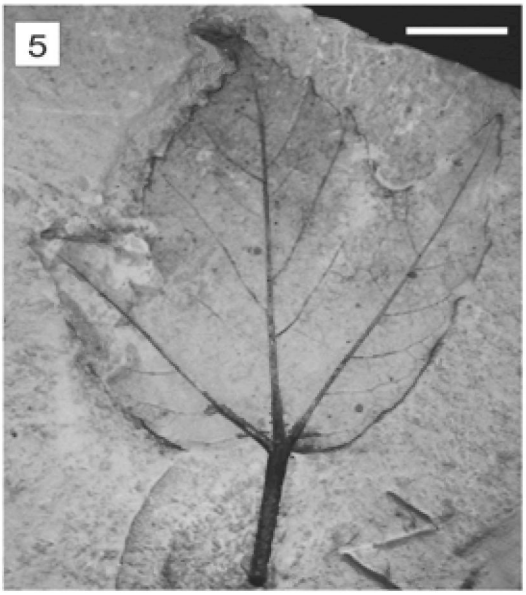
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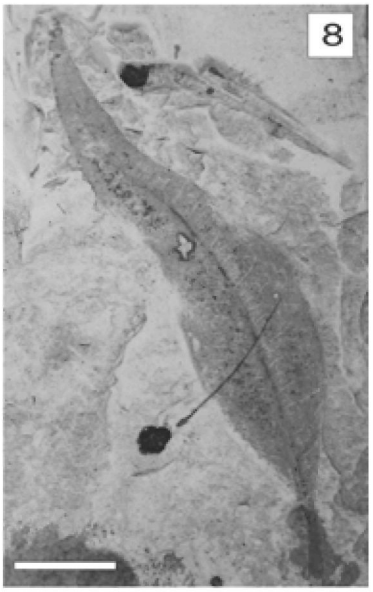
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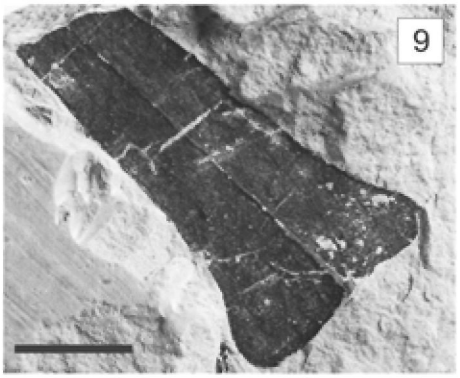
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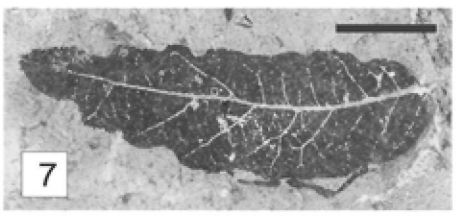
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